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A study of the transfer of sodium ions in relation to the ion migration potentials in the production of the action potential of nerve tissue, utilizing radioactive tracer techniques.

Bennett, Walter F. V.

Ohio State University



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MASTER OF SCIENCE
THESIS
LCDR. WALTER F. V. BENNETT USN

Thesis
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A STUDY OF THE TRANSFER OF JUNCTION IN RELATION
TO THE ION MIGRATION POTENTIALS IN THE PRODUCTION
OF THE ACTION POTENTIAL OF NERVE TISSUE, UTILIZING
EVALUATIVE TUNING TECHNIQUE.

Abstract of
A Thesis

Presented in Partial Fulfillment of the Requirements
for the Degree of Master of Science

by

Walter F. V. Bennett, B.S., U.S.N., M.Sc.

The Ohio State University

1961

Approved by

Adviser

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A STUDY OF THE CONCEPT OF SODIUM IONS IN RELATION TO THE
ION MIGRATION POTENTIALS IN THE PRODUCTION OF THE ACTION
POTENTIAL OF NERVE TISSUE, UTILIZING RADIOACTIVE TRACER
TECHNIQUE.

DAVID F. V. SWEET, LCDR., USN

B.Sc., Manhattan College, New York, 1942

Department of Physics

(approved by Ralph W. Stacy)

The inadequacy of the Membrane Theory, of nerve potentials, to explain the magnitude and phase reversal of the Action Potential in nerve, has resulted in a proposed modification, the "Sodium Shift Theory." Resting nerve is preferentially selective to potassium ion and impermeable to sodium. During activity, it is held that the selective permeability shifts in favor of the sodium.

Theoretical considerations, of diffusion and electric field forces, predict an ionic current across a permeable membrane separating two unequal concentrations of the same cation, providing anion mobility is regarded as zero.

The object of this research was to investigate the existence of sodium transfer across the nerve membrane during the conduction process and to correlate the magnitude of this ionic current and that of the associated action

A series of four lectures on the history of the
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potential assuming accepted values of the membrane parameters of resistance and capacitance.

Salt-fibred sciatic nerves of two subject groups were utilized; 14 leopard frogs (*Rana pipiens*) and 12 bull frogs (*Rana catesbeiana*). Radioactive tracer techniques were employed to determine the amount of sodium uptake, utilizing the isotope Na^{24} in well buffered Ringer's solution. Nerves were stimulated at 100/sec for three different time intervals.

The results were constant and reproducible, with a positive uptake of sodium per mg. of wet tissue determined in 24 of the 26 cases studied. The following conclusions were reached.

1. A sodium ion current does exist across the membrane of the nerve fibre during the conduction process as predicted.

2. The rate of entry as determined was 30×10^{-11} moles of $\text{Na}^+/\text{cm}^2/\text{sec}$ during the rise time period. The calculated ionic current was $0.0076 \text{ a.m.u.}/\text{cm}^2$.

3. The value of the membrane potential associated with this ionic shift was calculated at 32.3mv., half the magnitude required to account for the potential phase reversal. It is felt, however, that a parametrically similar biophysical system is in operation.

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A STUDY OF THE TRANSPORT OF SODIUM IONS IN RELATION
TO THE ION DIFFUSION POTENTIALS IN THE PRODUCTION
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Adviser

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PRESENTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

BY

WALTER E. D. DUNN, M.A., F.R.S.E.

THE LONDON SCHOOL OF ECONOMICS

AND

APPROVED BY

1914

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SECTION I INTRODUCTION AND REVIEW OF THE LITERATURE

The immediate objective of this experiment is to study the transfer of sodium ions across the nerve cell membrane during the conduction process with the view of correlating this magnitude of transfer as a function of the ionic or diffusion potential and as a component in the production of the action potential, utilizing radioactive tracer techniques.

The year 1786 witnessed the first recorded experiment in relation to the physics of the nerve conduction process. Luigi Galvani, a young professor of anatomy at the University of Bologna, demonstrated the now classic experiment of producing an excitatory response in a frog's leg when touched by two dissimilar metals. At the time, and as so often the case in the annals of science, the discoverer had a misconception as to the reason for the phenomenon he was observing. Galvani attributed the effect to "animal electricity." Another Italian, Alessandro Volta took issue with Galvani's conclusion and in 1800 showed that the essential phenomenon was not tissue dependent but a function of the dissimilarity of the two metals concerned. With the advent of the voltaic cell, classical physics arrived at one of its brightest and most productive eras. Simultaneously, the stage was set for the investigation of one of the most challenging problems in the combined fields of physics and biology or biophysics as we know it today.

[illegible][illegible]

In the testimony of this challenge we note as we review the early literature of experimentation in this field of nerve conduction, the appearance of names of men who were considered pioneers in the classical physics. As a physicist, Helmholtz is well known for his basic work on potential theory. However, in his application of physical principles to the problem of nerve function, he initiated the first of a series of studies to determine the velocity with which a nerve impulse was propagated as well as the electrical effects accompanying it. Both H. Weber and L. Hermann made extensive analytical investigations of the flow of electric current in conductors of cylindrical form in an attempt to better understand the phenomenon of nerve excitation and conduction. (2) We note that no sooner were classical physical concepts accepted as valid, they were applied in experimental work in an effort to produce a satisfactory explanation to the nerve conduction problem. For example, the year 1827 witnessed the development of Ohm's law and within a period of months experimentation was being carried out in an effort to see if the law were applicable to impulse transmission in nerve tissue section.

The year 1843 witnessed the demonstration by Du Bois-Reymond of the flow of a current of injury, in a nerve section, in the direction from an uninjured to an injured point. This experiment placed future inquiry on a quantitative basis in much the same manner as Faraday's laws of

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electrolysis affected research in electrochemistry after they were stated and accepted. Some ten years later H. Von Helmholtz published a general theory of bioelectric currents in which he showed that measurements of potential difference between two points on the surface of a nerve section will not be sufficient to determine the location or the nature of the electromotive forces that maintain the flow of the injury or demarcation current. A proper definition of this force had to be obtained by other than a surface potential measurement. Helmholtz recognized the nerve conduction problem to be a difficult one where the approach would have to be multiple, with ample use of all available tools of mathematics, physics and chemistry.

Prior to further discussion and for purposes of orientation we refer to Appendix A of Section VII. Diagram No. 4 is that of the longitudinal section of an isolated nerve fibre. What is ordinarily referred to as a nerve is actually a large number of these fibres. The fibres are of two general types, the medullated and the non-medullated depending on whether or not they possess a myelin sheath. The functional portion of the fibre is the axis cylinder which is protoplasmic in nature, a colloidal system possessing organic and inorganic electrolytic components, with water as the dispersing medium. The myelin sheath is in turn covered by a thin connective tissue membrane called the neurilemma. The fibres are organized into groups or bundles,

[illegible]

which are covered by a sheath of connective tissue called the perineurium. These bundles are located in a matrix of connective tissue which is referred to as the epineurium. (5)

Experimentation in the past has principally utilized nerve sections such as the frog sciatic which will contain on the average several thousand of these nerve fibres with a fibre diameter ranging from 0.005 mm. to 0.01 mm. (6) In recent years adequate micro dissection technique has permitted the use of the single nerve fibre such as the giant axon of the squid.

In a generally accepted sense, the function of the nerve is twofold. It generates a transient disturbance at the point of stimulation and propagates this disturbance along its entire length to a receptor organ. Whether excitation takes place by artificial means or by the natural process, the neuron always responds in exactly the same way, i.e., by conduction of a single impulse or a series of impulses. This impulse is invariably accompanied by an action potential, which we will presently define, and the only reliable method for the detection of the presence of this impulse is by means of a record of the action potential. As we shall presently note, studies of the nerve impulse have, for the most part, been made on excised nerves stimulated by means of an electric current. Actually other stimulation agents have been utilized in the past, namely pressure, light of a high intensity and specific wavelength

(7)

and chemical agents. The conduction process in nerve obeys the "all or none law", in that the quantity and intensity and duration of the stimulating agent must meet specified requirements before the nerve will initiate and conduct an impulse. Some authors will refer to this as the "law of Specific Energies", although this latter term is usually interpreted as to refer to the quality of the stimulus rather than the quantity. In the case of electrical stimulation, the voltage across the electrodes must of necessity be of a certain maximum value and it must change with a certain frequency such that the stimulating current will also change with respect to time in order that the nerve stimulation threshold be reached. The energy expended in propagation is released all along the nerve and is not derived from the stimulus. As in the case of muscle, a refractory period exists for the nerve. The period is subdivided into an absolute portion, during which a stimulating agent no matter how strong or specific will fail to initiate a response in the nerve tissue, and a relative portion in which a more specific than normal stimulus is required to initiate the conduction process. (8) The absolute value for the refractory period for the sciatic nerve of the frog is, for example, 0.02 sec.

The impedance elements of nerve are bi-directional in that an impulse in an excised nerve section travels in both directions from the point of stimulation although normally

in the *in situ* case the impulse is unidirectional due to the general synaptic arrangement which nature has provided.

Some five years later, in 1848, DuBois-Raymond stated that excitation in nerve was a function of the time rate of change of the current density. Since that time, that relationship has been verified for almost every known irritable tissue examined. (10)

Raymond failed to carry his experimentation on to any further significance principally due to the lack of sensitive recording instruments. Adrian stated the problem of the period quite well when he said, "The history of electro-physiology has been decided by the history of electric recording instruments." (11) The period of the latter part of the nineteenth century was therefore one of great technical difficulties. The currents, associated with the conduction process were extremely small and during the course of activity, would fluctuate very rapidly. The early research depended to a great extent on the mirror galvanometer which will show a current change but the inertia factor together with the fallibility of the human judgement introduced errors of considerable magnitude. As a result, indirect evidence was resorted to, which resulted in bitter controversies in the question of the proper interpretation.

The first attempt to obtain a record of the monophasic action potential was made by a German physiologist, L. Hermann, in the year 1851. Utilizing a group of capillary

As the latter was the subject of investigation the
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electrometers with a trusted observer on each instrument and after a large number of trials, the data was reconciled. The potential drops between the electrodes were computed and the curve was drawn. Lorente de No shows some tracing of the monophasic spike of the action potential, which were produced by Hermann, in his Rockefeller report. (14) While they were, no doubt, specially selected, this writer was deeply impressed with the resulting accuracy when we consider the technical problems which were involved. L. Hermann treated the nerve as an inert core conductor and proposed a theory to account for the existence of the electromotive force was created by the injury itself.

In the year 1902, a hypothesis was put forth by J. Bernstein to explain the existence of this electromotive force. Apparently Bernstein was deeply impressed with the electrolytic dissociation theory as advanced by Svante Arrhenius in Stockholm some fifteen years before. Bernstein regarded the nerve membrane as having the property of selective permeability, allowing certain ions in and rejecting others. It should be appreciated that he suspected that these ions would vary in size and that he had, of course, no means of determining the size of the ions concerned. Nevertheless, armed with the knowledge of some collateral information together with the phenomena which was observed, he proceeded to detail a theory which would explain qualitatively the origin and nature of the observed

conf. He considered the nerve membrane as permeable to the Potassium ion but impermeable to the Sodium cation and anions in general, with the difference in the Potassium concentrations in the interstitial fluid and the interior of the nerve, responsible for the resting membrane potential. As a result of this selective permeability, the Potassium ions will form a layer of positive charges on the border of the cell membrane and just beyond. The anions which are present in the axoplasm will form a similar layer just within the membrane, the net result being a double layer, separated by a membrane and thus exhibiting a difference in potential. Thus he regards the axoplasm as negative and the interstitial tissue fluid as positive. Bernstein thus accounts for the current of injury being initiated as a result of the local damage or rupture of the membrane. The potential difference preexists and on membrane rupture a current flows in the outer circuit from the intact surface as a positive pole to the injured area as a negative pole. (14) Bernstein's theory has often been regarded as correct in essence as a definition of the resting membrane potential with a wide reference made to it in the literature. Today it is known more specifically as the Membrane Theory. While the theory does possess limitations which will be discussed later in this section, some recent experiments have advanced rather conclusive evidence in favor of the membrane theory. (15)

J. Macdonald in 1902 conducted significant experiments with the injury potential of medullated nerve. He found that by increasing or decreasing the concentration of Potassium in the bathing solution there was a direct effect on the magnitude of the action potential observed. He noted a logarithmic relation between the concentration of the Potassium ions outside the nerve and the concentration inside the nerve. This contribution was made about the same time that Bernstein formulated his hypothesis; nevertheless the literature attests that Macdonald was the first to state that the relative Potassium concentrations in the axis cylinder and the tissue fluid were responsible for the injury potential. (16) At the time of publication of the report of Macdonald's work, he was criticized for failure to maintain his bath solutions isotonic with that of tissue fluid as he varied the Potassium concentrations. Then too, he did not make any allowance for the osmotic pressure effect nor were any references made to the condition of his nerves, upon completion of his runs. For that failure of omission, the findings were taken somewhat lightly at the time but in the years to come his work stood the test of duplicated inquiry to the extent that his results are considered valid.

In the year 1908, Bernstein in a more detailed treatment (17) suggested that the nerve fibre and the external fluid represented a system in equilibrium. He postulated

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that the membrane potential was a phase boundary potential similar to the boundary potential which appears at the boundary between two immiscible solvents when an electrolyte solution having different activity coefficients distributes itself between the two solvents. Nernst carried his ideas further on the basis of dynamical considerations and developed his well known equation for the diffusion potential

$$E = \frac{RT}{F} \frac{(u - v) \log_e \frac{C_1}{C_2}}{(u + v)}$$

where u represents the cation mobility and v is the anion mobility. Nernst assuming that the anions were immobile, set v equal to zero and used Nernst's equation as an expression for the membrane potential which will now appear as,

$$E = \frac{RT}{F} \log_e \frac{C_1}{C_2}$$

On proper substitution in the foregoing equation with the value of R of 8.314 joules per mole per degree, with an F value of 96,500 coulombs per Faraday of electricity and suitable conversion to the base ten log scale, the following simple expression results, at 18° Centigrade,

$$E = 58 \log_{10} \frac{C_1}{C_2} \text{ mv.}$$

We now consider the mechanism proposed for the action of this potential during the conduction process. Consider a finite length of a single nerve fibre. The extreme right end is reference point B and the midpoint of the fibre is point A . We place two electrodes at these points with sim-

ilar designation. The point B end is then injured by crushing. A sensitive voltmeter is placed between electrodes and the resulting reading will indicate point A as positive to point B. This potential difference is that indicated by the foregoing membrane theory considerations. Consider now two stimulating electrodes placed to the extreme left end of the nerve section. Upon stimulation, a change in permeability occurs beneath the electrodes and due to the potential difference between the outer and inner membranes, an action current takes place in an inward or coreward direction. The impulse then travels to the right along the nerve. Upon reaching the recording electrode at A, the two points A and B are then isopotential. As the impulse travels further on, the membrane beneath the electrodes at point A regains their insulation function or repolarize and point A becomes positive to B once again. A record of this transient variation of potential as the impulse travels over the nerve is called the action potential and in this particular case it is identified as a monophasic type. (15)

Similarly, we may consider a nerve section which is not crushed but two electrodes are spaced an equal distance apart from the midpoint of the length of the fibre. From left to right as we observe the nerve we identify them as electrodes A and B. At the extreme left end of the nerve section we place a pair of stimulating electrodes and commence stimulation. The membrane beneath the stimulating

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electrode depolarizes as before and when the impulse reaches the vicinity of electrode A, the electrode A will go negative with respect to the B electrode. As the impulse passes and the membrane beneath A comes back to its polarized state, A then resumes its isopotential relationship with respect to B. When the impulse reaches the point C, the inverse portion of the wave is executed. In a potential versus time plot, this transient condition would represent itself an inversion of a sine wave. This type of record is called a diphasic action potential.

In view of the foregoing explanation it would seem that the action potential could not be larger than the magnitude of the resting potential. This was the opinion of the "membrane potential" school for many years and was in fact accepted until 1940. (19)

At this point we will introduce a refinement of the definition, action potential. It has been observed by experiment that the action potential was composed of several component parts and not limited to one smooth variation, but including not only the event discussed above but also positive and negative after potentials. The potential wave to which Bernstein et al referred is now designated in the literature as the spike potential. The above monophasic and diphasic variations are properly called the monophasic and diphasic spike potentials. (20)

In 1918, L. Buzsáki introduced his membrane model in an

effort to account for the membrane potential. The model consisted of aqueous solutions separated by a layer of immiscible liquid. ^(21,22) He has taken the license to extrapolate this phenomenon to living systems. In one of his earlier models which may be described as 0.1 N KCL/salicylic aldehyde and salicylic acid/0.0003 N KCL, he was able to report a membrane potential of 100 mv., with a positive charge existing on the membrane side of the lower concentration. By variation of the concentration of the solution on the left, the negativity increased. In similar experiments he utilized mono and divalent anions but retained the same cation Na., with the same result. Beutner's logic in reasoning the nature of the forces operating or the factors involved are somewhat confusing. He tends to believe the charge distribution is a function of the partition of the ions in the respective solvents with the idea of a concentration cell in mind. However, he repeatedly adheres to the idea that the organic film or pseudo membrane is responsible for the emf of this and living systems. To quote from Lorente de No, "Beutner's concept of the nerve membrane is difficult to follow". ⁽³⁾ Since 1912 and up to the present time, Beutner in collaboration with T. Cuncliffe Barnes has repeated his model experiment with numerous variations for the organic interface and with variations in solvent salt concentrations with interesting results for membrane potentials. ^(23,24,25,26) In a more recent experiment, Beutner and

Barnes have found that Acetylcholine, a physiologically important organic compound has a marked effect on the potential difference of an oil saline interface. (27) This work is significant in light of further consideration of the function of metabolism on the maintenance of the resting potential.

In the period just prior to the first World War, the application of vacuum tube amplification to nerve conduction and potential study was made by Dr. Keith Lucas of Trinity College, Oxford. By means of this advance, Amberson and Downing made the first report on the components of the action potential having noted the positive after potential in a monophasic wave. (28)

The years that followed the war saw the application by Erlanger and Glasser of the cathode ray oscilloscope to experimental study. In their work the results of Amberson and Downing were verified, and in many respects amplified. They conducted a thorough study of the spike components due to the class of fibres participating in the conduction as observed in a transient wave pattern. (29,30) In a later experiment Douglas et al worked out the preliminary correlation between fibre size and potentials observed. At a later date, this work was consolidated by Gasser and Grundfest wherein they showed a higher potential value and a higher conduction velocity in proportion to the axon diameter. (31)

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In the mid twenties, H. Hille and his introduction of the passive iron wire model as a parallel to the conduction process and Michaelis with his work on the colloidin membrane added weight to the membrane theory. (20, 24)

The membrane used by Dr. Michaelis was a partially dried colloidal membrane which exhibited a marked selectivity to ions, allowing the cations or anions through respectively depending whether or not the pores of the membrane were negatively or positively charged. If one may regard the nerve membrane to possess negatively charged pores, we have a system postulated by the Bernstein theory.

In the early thirties, experimental effort proceeded along the lines of two major subdivisions, namely that of the physical and that of the chemical aspects of the problem. Significant studies, which assert that a metabolic and chemical process operates in some phase of the conduction phenomena, were made by A. V. Hill and R. W. Gerard. (25, 26)

The position of metabolism function was strengthened by reports of increasing oxygen consumption by nerve during activity and the effect of metabolic inhibitors on the resting potential as reported by Loewen. (27)

In 1936, Dr. Bachmann first introduced the idea of the association of acetylcholine with the conduction process. His work significantly correlated chemical energy equivalents to account for the corresponding electrical energy of the action potential and introduced the time factor consider-

ation for the first time. The attention to the chemical aspects of the problem increased when T. C. Barnes in a more recent report of his work on organic interface model system, (39) stated:

".....In conclusion it would appear that the basis of nervous energy resides in the phase boundary electrical potential generated by compounds in the nervous system containing tetravalent nitrogen of which the outstanding example is acetylcholine."

Still more recent work, of only a few short weeks ago, of Eyring and Johnson, (40) states that the source of energy for the potential difference of the resting state of the membrane is due to the metabolic production of acids from non-electrolytes such as glucose. Eyring states a belief that:

"The differential rate of escape of H⁺-ions and organic anions through the semipermeable membrane maintains the potential....Upon stimulation, increase in permeability permits freer diffusion and a reduction in the potential difference which, in nerves, is then quickly restored by the rapid production of acetic acid from acetylcholine through choline esterase activity."

Unfortunately the abstract states no more than a theory which has often come to mind of a good many workers in the field during the past ten years. It represents a desirable reconciliation of two divergent points of view but the more curious of us would like to see the experimental data and proof.

In the six year period prior to the second world war, a continuous study was made on the electrical characteris-

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ties of the nerve membrane. The terms membrane resistance, conductance and impedance began to make their appearance in the literature. Curtis and Cole^(5,41,42) made successful measurements of the impedance of both vitella and the giant squid axon membrane utilizing the balanced A. C. Wheatstone bridge with leads to the vertical deflection plate terminals of an oscilloscope. By means of mathematical manipulation, the impedance is expressed as a function of the bridge parameters.⁽⁴³⁾

At this time extensive theoretical consideration was given to describing the various aspects of the stimulation problem taking departure from the fact that the potentials were assumed and expressing the rheobase, and stimulation threshold as functions of voltage, charge density and time. Much of this work had to be revised in light of developments in 1940.

In 1940, Kenneth Cole and H.S. Curtis perfected a technique for using micro electrodes for insertion into the axoplasm of the giant squid axon. By measurement of the action potential utilizing two electrodes, one external and one internal it was noted that the transient wave was as shown on Diagram A-5. It was noted that the outer surface electrode not only went to zero potential with respect to the inner electrode but also swung strongly negative.⁽¹³⁾ This actually represents a complete reversal in phase and is not predicted by the capacitative aspect of the

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entrepreneurs exhibit low levels of risk aversion.

As this line extends laterally, it divides the

polymer will be removed completely and completely re-oxidized.

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is the result of analysis of the full data set. The results are shown in Table 1.

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and the directorates of London and the South East.

the Committee has, however, not identified a sufficient number

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will be the same as the one for the first case.

membrane theory. The magnitude of the action potential was as great as 100 mv. while the injury or membrane potential was rarely greater than 55 mv. This points up an inconsistency in the membrane theory which predicted that the action potential could never be larger than the membrane potential. This work of Curtis and Cole was duplicated at the same time and independently in England by Alan Hodgkins and A.F. Huxley with confirmatory results.

The experimental results definitely demanded a revision of the membrane theory to account for this observable overshoot or phase reversal. In 1941, Cole discussed the possibility of an inductive element in the nerve membrane being responsible for the overshoot as for example in the conventional oscillatory circuit, basing the existence of a membrane property as a parallel to the piezo electric crystal reaction. (46) This idea was not pressed too deeply but was rather well thought out by Cole.

Today the problem of accounting for the magnitude of the action potential still remains a challenge. However, Hodgkins and Hatz feel the reversal of the membrane potential during the action potential can be explained on the basis of a change in the selective properties of the membrane during certain periods of the conduction process. (47) The resting membrane is held to be more permeable to potassium than to sodium. On stimulation there exists a permeability shift such that the membrane becomes highly

permeable to the sodium ion. A reversed membrane potential can arise in a system of this type providing that the concentration of the sodium in the external solution is greater than the concentration in the axoplasm. With this in mind, the research phase of this thesis was directed. If at all possible, it will be our aim to correlate the transfer of the sodium ions with the magnitude of the action potentials. To do this we will apply the theoretical considerations of the diffusion equations of Teorell and Goldman with modifications to be presently described. (48,49)

The author wishes to express his deep appreciation to Dr. Ralph W. Stacy, under whose direction this work was done, for the assistance and guidance given him; Dr. Eric Ogden for his thoughtfulness and cooperation; and to Dr. W. G. Myers for his suggestions and procurement of the required isotopes of sodium from the Oak Ridge National Laboratories.

SECTION II METHODS AND FACILITIES

A preliminary consideration prior to experimentation was that of selecting one of two available isotopes of Sodium, Na^{22} produced by $\text{Mg}^{24} (d, \alpha) \text{Na}^{22}$ reaction with a $T_{1/2}$ of 3.0 years, and a decay scheme; (57)



or Na^{24} produced by a $\text{Na}^{23} (d, p) \text{Na}^{24}$ reaction with a $T_{1/2}$ of 15.1 hours and a decay scheme; (58)



While use of Na^{22} would facilitate decay computations, the decision was in favor of use of Na^{24} . The relative higher energetic beta emission was desirable from the view of the smaller self absorption counting loss of samples. Then too, the longer half life of Na^{22} with $T_{1/2}$ of 3.0 years would demand a more extended disposal and decontamination technique in the event of an accidental spill.

The isotope Na^{24} was made available by Dr. H. L. Pool of the Physics Department of Ohio State University by means of cyclotron bombardment. Later arrangements were made through Dr. William G. Myers of the Ohio State University for procurement of Na^{24} from the Isotopes Division of the Oak Ridge National Laboratories.

In view of the gamma emission of 2.753 and 1.390 Mev for the Na^{24} isotope, extreme care was exercised in dilu-

tion techniques and the degree of shielding employed. The gamma quantum dosage rates were calculated on the basis of the relation $Rf = 6 CG$ where G is the activity in millicuries, E is the average quantum energy in Mev and Rf is the dosage rate in milli-roentgens per hour at one foot distance unshielded. (58)

The degree of shielding to be used was calculated by the usual exponential relationship.

$I = I_0 e^{-ux}$ where I , I_0 , u and x have their usual significance. For lead and red brick, the following absorption coefficients were utilized.

Energy (Mev.)	Pb (59)	Red brick (70)
1.39	0.52 cm. ⁻¹	0.115 cm. ⁻¹
2.71	0.47 cm. ⁻¹	0.0326 cm. ⁻¹

Upon completion of calculated requirements and erection of the shielding material, the area about the shield was always monitored by means of a portable ionization chamber calibrated to read in mr. per hour in order that the calculated dose rate may be checked.

The activity of all radioactive shipments was determined upon receipt. In case of Oak Ridge shipments a comparative check was thus made with the activity reading on the shipping bill. For the case of the Na^{24} received from the Ohio State University cyclotron, an assay had to be made to determine the activity. The true activity of the sample was determined by application of the geometry factor g_p , to the count rate computed from the total mea-

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bar of counts and the elapsed time or in equation form.

$$\text{No. of nc.} = G_f(\text{cm/st})_{sc} / (2.7 \times 10^3)$$

This relation checked accurately with shipment data of the isotope shipments. The factor G_f , of course, was determined for a constant geometry of the assay sample holder by comparing the recorded activity of a standard reference source with the activity of the source as determined by our counting equipment.

We were in effect provided therefore with two methods of a scaling circuit check. Thus daily, prior to counting, the auto scaler was checked against line voltage and secondly, the gauger tube and scaler were checked for a constant geometry factor. This factor fortunately remained constant all during the experimental work.

The arrangement of the experimental equipment was as shown in the schematic and photographs of the appendix. The stimulation isolation unit was inserted between the stimulator and the stimulating electrodes to reduce the stimulus artifact to a minimum so the nerve action or spike potential might be more clearly seen on the oscilloscope. The purpose of the oscilloscope in this experiment was purely for monitoring the viability of the stimulated nerve.

On receipt of the air shipment of the Na^{24} from Oak Ridge the shipment box was placed under a hood. To the

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solid salt, 15 ml. of Ringers solution was added. The salt was quickly put in solution by mechanical mixing and the solution was then transferred to a glass bottle and placed in a portable lead container. The target solution, so called, was now ready for assay. Since the number of grams of NaCl shipped was known, the number of Sodium ions in solution could be easily calculated.

Where the Na^{24} was obtained by deuteron bombardment from the cyclotron, the procedure was slightly modified. The copper target used for the bombardment was accurately weighed prior to loading with salt (NaCl). Upon receipt of the target from the cyclotron, the target plus salt was weighed. This was done behind appropriate shielding and with constant monitoring technique. The amount of salt was obtained by difference. The target and salt was then placed in 5 ml. of Ringers solution and allowed to stand for fifteen minutes.

In the assay of target salt solutions, usually 0.2 ml. of solution was withdrawn by remote pipette and this 0.2 ml. was diluted to 100 ml., one ml. of which was counted. The activity of the initial solution was thus obtained. A sufficient amount of target or initial salt solution was then withdrawn by remote pipette and diluted to provide a working solution of 1000 cps. per ml. Usually 100 to 150 ml. of working or bathing solution was prepared and stored in the aspirator bottle within the lead

shielding. (Note Appendix C-1.)

The nerve stimulation platform was specifically designed for this experiment. Four parallel wire troughs were milled out in a rectangular block of lucite 81 mm. x 20 mm. x 7 mm. The troughs or guides extended longitudinally 81 mm., 0.75 mm. wide, 1.4 mm. apart and were cut to a depth of 3.5 mm. A rubber stopper fitted with four holes to meet the milled wire guides of the lucite platform, was attached to the butt end of the lucite block by a small "L" type copper flange. Note picture No. 3 of Appendix C. Number 30 gage Platinum wire with a resistivity of 10×10^{-6} ohm cm. or 1.959×10^{-2} ohms per cm. of length at 20° C. was used. The wire was embedded in the guides by means of a clear plastic insulation cement. The electrodes were fashioned by two simple 90° bends and set 3 mm. apart prior to the setting of the cement. The second set of electrodes were similarly spaced in the guides and cemented in 24 mm. from the first electrode set. A small lucite plate served to spread the platinum wires as they exited the rubber stopper and terminated at the electrical terminals preset in the plate. This plate was connected to the stopper by the usual "L" type copper flange. The unit was then given a standard insulation resistance test and the results were in the vicinity of 1000 megohms. Throughout the experiment the unit functioned very satisfactorily with the electrodes salting out on

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just one occasion. This was to be expected in view of the constituents of the bath solution. Consequently the practice was established of cleaning the electrodes upon the completion and prior to the start of a run.

Two species of frogs were used to obtain sections of sciatic nerve. Fourteen experimental runs were made with the leopard frog, *Rana pipiens*, and twelve runs were made with the giant bull frog, *Rana catesbeiana*.

The animals were handled in the following manner. The frogs were sacrificed and both sciatic nerves were carefully excised using normal dissection techniques. The nerve was carefully cleaned of all small blood vessels while in situ and upon excision were placed in cold bloodedingers solution. Careful handling of the tissue section was mandatory, to avoid any damage to the nerve.

The nerve sections were then arbitrarily designated the stimulated section and the control section and then placed on the nerve platform. The control nerve was attached by thread at the extremities to the attachment runs of the nerve platform. The experimental nerve section was similarly attached but racked over the platinum electrodes on the electrode side of the platform. A slight degree of tension was required in case of the experimental nerve in order to insure a good electrode contact. This tension was duplicated for the control section.

after placing nerve sections on the electrode platform, the unit is then set into the nerve chamber at D (Appendix A-1). The petcock at the left opened, the right and lower petcocks closed, allowing cold blooded Ringers to enter and rise in the nerve chamber. When the meniscus of the Ringers solution covers the entire length of the nerves, the left petcock is secured. At this time the requisite electrical connections are made. The nerve is stimulated at a frequency of 100 impulses per second with an impulse duration of 0.5 milliseconds. The oscillograph is monitored for the action potential. After the action potential or rather the spike is observed, the lower petcock is opened and the nerve chamber is drained of Ringers solution. The chamber is then filled with the Ringers solution containing the radioactive tracer component. Both nerves are immersed in the bathing solution for a period of thirty minutes prior to stimulation in order that surface adsorption phenomena will arrive at the equilibrium point.

Stimulation rates of 10 min. and 40 sec., 20 min. and 20 sec., and 30 min. were assessed, with the stimulation total at 100,000, 200,000 and 300,000 stimuli respectively. The duration of stimulus was 0.5 milliseconds with a potential difference across the stimulation electrodes of 8 volts. The time of initial rise and termination of stimulation was monitored.

designated by t_4 .

Upon completion of the stimulation at t_4 , both nerve sections were rinsed with the non-radioactive Ringers solution for five consecutive rinses in order that the surface absorption might be minimized. After rinsing, the stimulated and control sections were removed from the electrode platform. The necessary lengths, approximately 8 - 10 mm. of nerve, were removed from the extremity of both nerve sections and placed in labeled vials containing ten percent formalin for purposes of preservation for later histological study. The residual portions of both control and stimulated sections were measured for length, and then placed on preweighed aluminum lined counting planchets. The nerves were spirally coiled in the planchet center for pattern uniformity. The times for determining the count rate of the control and the stimulated section were designated t_5 and t_6 respectively for purposes of recording data. Upon completion of the wet count, two drops of 2M nitric acid were added to the nerve sections and these were heated lightly to a slight residual ash. The count rate for both the experimental and control ashed samples was then made. The same type of time designator was used.

The bathing solution containing the tracer ^{45}Ca which was drained off at the termination of stimulation is then assayed. By means of the remote control pipette 0.5 ml.

of the bath solution is drawn off and diluted to 100 ml. One ml. of this diluted solution is counted. By proper calculations the activity of the bathing solution is determined.

As will be shown in the next section, all count rate determinations are corrected to one reference time, t_0 , in particular. Thus all decay corrections are applied to all count rates so the rates may be compared at the same reference time.

In the initial stages of development, we intended to determine the count rate on the basis of gamma emission, neglecting the beta by means of aluminum filters. However, in view of the higher beta efficiency of the counter tube compared to the gamma as was clearly brought out by a regular ^{24}Al aluminum absorption study, it was decided that the beta emission was definitely to be considered. The gamma count is included of course but since this is in the vicinity of 1% of the beta count, there is no concern over the procedure.

The possibility of a counting loss due to self absorption of the beta particles by the tissue ash was investigated. Nerve sections of variable weight were placed in aluminum lined planchets containing 1 ml. of a solution of a known activity. The ashing technique was carried out, on the completion of which, comparative count rates were made. Due to the small sections of nerve used and

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the short air path to open window, there was no significant difference noted. Therefore, it was decided that the self absorption loss correction could be neglected.

For purposes of histological study, the nerve sections were treated in the usual water, 70% alcohol, 80% alcohol, absolute alcohol, and chloroform stages with five hours in each stage. The sections were then placed in the paraffin biloid series at graduated temperatures and then imbedded in rubberized paraffin. The sections were then microtomed and slides prepared. By this means, the number of fibres in each nerve were determined. It was hoped at first that the diameter of the fibres might be determined by use of a Hausch and Lomb ocular micrometer but this proved unfeasible due to a shrinking of the nerve tissues during the immersion stage process of sectioning.

SECTION III RESULTS

Prior to the survey of the results of the experimental phase, we shall once again state the objective of this study. We are initially interested in the existence of a sodium ion transfer across the nerve membrane during the conduction process, the magnitude of that transfer, and the magnitude of the associated potential. We are interested further in a comparison between the computed value of the potential associated with this ionic transfer and that value of the magnitude of the action potential which is a matter of record in the literature.

It will be shown presently in Section IV that theoretical considerations indicate the existence of an ionic current density as a result of the action of two forces, one the result of a concentration gradient and the other due to electrical considerations of an existing potential gradient. We will examine the constancy of the computed value of the associated potential with a view toward the possible correlation of this value as a part of the total ion migration potential which is responsible for the ionic current as defined by equation VIII of Section IV.

In Table V of Section VII, the summary of computed data is listed. It is noted that runs 1 to 5, where the nerve sections were stimulated for a period of 16'40", show an average uptake of Na ions in the amount of

9.574×10^{10} ions per stimulus per cm^2 of membrane surface area. The series of nerves which were stimulated for a period of 35'20" show a comparable average value of 11.36×10^{10} ions per stimulus per cm^2 . In the third period of stimulation, that of 50', there is a marked falling off of the number of ions taken up by a nerve section. In this case the average value was 4.41×10^{10} ions per stimulus per cm^2 .

In graph B-2 of Section VII, which represents the uptake of sodium ions per mg. of wet tissue versus the time of stimulation, there is a strong indication of an operating force which is quite constant in function. It will be noted that with the time limits of zero to 35'20", the uptake is linear. In fact, in the case of the uptake for the nerve sections of the subject *Rana pipiens*, the computed values fell in so closely that no statistical analysis was warranted. The curve drawn on graph B-2(b), shows a linear relationship between uptake and stimulation time. However, in this case, there was a degree of scatter to the plot which warranted statistical consideration of the small sampling method technique. Apparently, there is an uptake which is linear with time and then a "fatigue" function sets in, which we shall presently discuss.

With reference to our initial consideration, then we note that an ionic migration has occurred across the surface area of the nerve and passed into the nerve

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tissue to a certain distance. We justify this conclusion on the basis of control considerations and the experimental results which show a positive uptake, in an overall survey, in 24 of 26 cases. This differential between control and experimental sections is well defined as shown in the data of tables I and II of the Appendix.

The number of moles of sodium which have entered the section per stimulus per cm^2 of surface area are given in the following tabulation, for runs 1 to 14 inclusive.

Run No.	No. moles of Na taken up by section per stimulus per cm^2 (Avg.)
1-5	1.589×10^{-13}
6-10	1.970×10^{-13}
11-14	0.752×10^{-13}

At this point we postulate, for reasons to be discussed later, that the increased permeability of the membrane to the sodium ions or the ionic migration occurs during the rising period of the action potential. From the literature we take the value of 0.456 msec for the rise time. Considering the time factor, the above ionic transfer may be expressed in terms of the number of ions which enter the membrane per second per cm^2 during the rising phase. In the following tabulation we have the expression for average rate of entry during this period.

Run No.	No. moles Na per sec per cm ² (Avg.)
1-5	34.9×10^{-11}
6-10	42.2×10^{-11}
11-15	16.95×10^{-11}

These values indicate a degree of constancy within the time limits of zero and 33'20" with a fall off rate of entry after the 33'20" period. The values are in fairly good agreement in magnitude with the theoretical value computed by Hodgkins and Katz in 1948⁽⁴⁷⁾ for the single nerve fibre of the squid, of 8.4×10^{-11} moles/sec/cm².

The time average for the ionic current computed by application of the Faraday value of 96,500 coulombs/mole to the above rates of entry, gives

Run No.	Milli-amperes per cm ² (Avg.)
1-5	0.0336mA.
6-10	0.0416mA.
11-14	0.0155mA.

The same values are obtainable by a time average of the coulomb transfer as shown in the Table V.

If we consider the potential requirements of a theoretical membrane condenser with a capacitance of 1.2×10^{-6} farads/cm² with no resistance considered, the following potential values are obtained.

Run No.	Potential Diff. (Avg.)
1-5	12.72mv.
6-10	15.82mv.
11-14	3.88mv.

It is readily appreciated, by inspection, that these values are of such a magnitude as to warrant disposal of the idea of a pure capacitive case from further consideration. It is to be noted that the first ten runs do maintain a degree of constancy in these calculations.

We next consider the case of the theoretical membrane condenser of 1.2×10^{-6} farads/cm² capacitance in series with a membrane resistance of 1200 ohms/cm². By means of equation IV-c of Section IV, the following potential values, which a membrane condenser would have to have, to discharge through a given resistance value in the known rise time equivalent, are listed.

Run No.	Potential Diff.(Avg.)
1-5	47.24mv.
6-10	58.60mv.
11-14	21.77mv.

The results of observed and computed values for the second subject group, the *Rana catesbeiana*, are included in Table II of the Appendix. The surface area determinations were made on the basis of an arbitrary value in this group inasmuch as the histological sections for this group were not ready for study and evaluation at the time of writing. The values listed in Table II indicate a trend but inasmuch as little or no analysis can be made, these values are not listed here.

In the case of the first group of fibres, a good approximation of the surface area could be made on the

basis of Hardesty's thorough investigation of the number and arrangement of the nerve fibres of frogs of this group type. This report indicates a mean of 4200 fibres in the sciatic trunk of the *Rana pipiens* in the 50 gram body weight range with a mean fibre diameter of 7.5×10^{-4} cm. These values were utilized in the computation of the surface area of the nerve sections.

SECTION IV DISCUSSION

THEORETICAL CONSIDERATIONS

(A) Dosage Evaluation

In view of the fact that the literature reports, (51,52) with a few exceptions, that radiation tends to increase the permeability of the cell membrane, it is necessary to evaluate the possible effect the levels of radiation, used in this experiment, had on the nerve section under study. Ordinarily, we would calculate the theoretical dose a tissue section would receive during an immersion period and then run control and experimental sections under stimulation in non-radioactive and radioactive solutions respectively. Any differential observed in permeability or conduction characteristics could then be correlated with the dose received and evaluated accordingly.

However, due to limitations of time, our procedure will be to calculate the maximum theoretical dose and compare this with the data available in the literature. It will be recalled that of all the common tissues, the nervous tissue possesses the least sensitivity to the particulate or electromagnetic type of radiation. (53)

In regard to data comparison, the work of Dr. A. Rothenberg includes information as to the dosage required to effect a change in the permeability of single fliored

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nerve.

To recall that Na^{24} on disintegration to stable Mg^{24} will yield a beta of 1.39 mev. and two gamma rays of 1.39 and 2.76 mev. energy per disintegration. In a theoretical dose calculation we must, therefore, calculate the dose received due to the two radiation components in the emission from Na^{24} . Inasmuch as we are to make our comparison based on the highest dose which any nerve section received in any one run, we select the highest value of the activity for any bath solution in the experimental data as set forth in Appendix VIII 2-3.

In run No. 20, a multifibred sciatic section was immersed in a bathing solution for 20 minutes with a count rate, uncorrected for geometry, of 4,240 cps. The expression for the activity in microcuries per ml is:

$$\text{Eq. (1)} \quad \mu\text{c.} = (dn/dt) f_g / 1.7 \times 10^4$$

where f_g is the correction factor for the geometry, air path absorption and mica window absorption. With $f_g = 73.6$, the activity becomes on substitution, 0.72 μc per ml.

In the determination of the number of roentgen units we shall first consider the dose received as a result of the beta emission. Consider a nerve section 30mm. in length and 1mm. in diameter placed on the nerve platform, the thickness of which is 7mm. In view of the fact that the maximum range for the betas of the Na^{24} emission is 8mm. in water, the calculation will be simplified if we

consider the beta emission from the solution on the other side of the nerve platform as completely attenuated.

The average energy available per ml. of solution will be.

$$\text{Eq. (II)} \quad \bar{E}_\beta = 5.7 \times 10^4 u \bar{E}_\beta$$

where u represents the isotope concentration in $\mu\text{e/ml.}$ and \bar{E}_β equals 0.48 mev. the average energy of the beta particles. The total dose received by the nerve section for a period of time of 80 minutes may be found from the expression, (64)

$$\text{Eq. (III)} \quad D_\beta = 5.7 \times 10^4 \bar{E}_\beta \int_0^z \int_0^v u \, d\text{vdt/nr}$$

where u retains its above significance, g is the geometry factor, n is the number of ion pairs formed per gram of air per roentgen and W is the energy equivalent in electron volts per ion pair. On substitution and integration, the dose due to the beta component of the radiation will be 180 mr. at any point on the surface of the nerve section.

The calculation of the surface dose received at any point by the nerve section as a result of the gamma component of the emission spectrum is determined by the theoretical treatment of Marinelli and Hines. (65) For purposes of symmetry we will calculate the dose rate and then the integral of this function over the time run at a point on the surface of the nerve section midway between its ex-

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tremities which we designate as point O.

The following equation represents the dose rate calculated at the surface at point O

$$\text{Eq. (IV)} \quad d_r = \int_0^V \frac{I c e^{-uR}}{R^2} dV$$

where I_γ is a function of the number of gamma rays emitted per disintegration, the linear absorption coefficients for Compton scattering, photoelectric and pair production effects. The quantity c is the concentration of isotope in mc. per ml. of solution. R is the distance between an element of volume dV and the point O. The term u represents the linear absorption coefficient of the bath solution.

The total dose is then expressed as:

$$\text{Eq. (V)} \quad D_r = \int_0^T d_r dt$$

On substitution and solution, the calculated surface dose for a nerve section due to the gamma components of the radiation is expressed as:

$$\text{Eq. (VI)} \quad D_r = \sum_J (I)_J c \int_0^T \int_0^V \frac{e^{-uR}}{R^2} dV dt = 1.74 \text{ Roentgens}$$

where J takes value 1 and 2 since two gamma rays are emitted in the disintegration process. The integrand in this solution is solved by a first term series approximation. This is valid inasmuch as the linear absorption

consequence of the fact that the function $f(x)$ is not continuous at $x=0$. The following theorem expresses the fact that the function $f(x)$ is not continuous at $x=0$.

$$\lim_{x \rightarrow 0} f(x) = \lim_{x \rightarrow 0} \frac{1}{x} = \infty$$

Proof. Let ϵ be a positive number. We choose $\delta = \epsilon$. Then, if $0 < |x| < \delta$, we have $|f(x) - \infty| < \epsilon$. This shows that $f(x)$ is not continuous at $x=0$. The function $f(x)$ is not continuous at $x=0$ because it does not have a unique limit as x approaches 0. The limit of $f(x)$ as x approaches 0 is ∞ , which is not a real number. The function $f(x)$ is not continuous at $x=0$ because it does not have a unique limit as x approaches 0.

The above theorem is a special case of the following theorem.

$$\lim_{x \rightarrow 0} \frac{1}{x} = \infty$$

Proof. Let ϵ be a positive number. We choose $\delta = \epsilon$. Then, if $0 < |x| < \delta$, we have $|f(x) - \infty| < \epsilon$. This shows that $f(x)$ is not continuous at $x=0$. The function $f(x)$ is not continuous at $x=0$ because it does not have a unique limit as x approaches 0. The limit of $f(x)$ as x approaches 0 is ∞ , which is not a real number. The function $f(x)$ is not continuous at $x=0$ because it does not have a unique limit as x approaches 0.

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coefficient for water, in case of gamma, holds quite close to 0.05 cm.^{-1} in range to 0.1 to 3 mev.

In summation we calculate the total dose in roentgen equivalent physical units to be 1.87 R. at the surface of the nerve section. In view of the approximations which have been made in these calculations, with regard to geometry and beta absorption, this value represents an upper limit. An evaluation of the possible effect a dose of this magnitude would have on the nerve function will be made in the latter part of this section.

(B) Action Potential and Ionic Current Density

It will be recalled from our review of the literature that the Bernstein theory of the membrane potential can account for magnitude and sign on the basis of relative ionic concentrations in the axoplasm and interstitial fluid, when these factors are introduced into the modified Nernst equation. Most research done to date on these relative concentrations places the ratio at a minimum of 10:1 with the majority of reports at higher values. When one substitutes this ratio into the modified Nernst equation the result of 58 mv is obtained. We recall that the membrane is positive with respect to the axoplasm.

It was demonstrated by Curtiss and Cole that the shift in membrane potential during the activity phase will be in general of the order of 60 mv to -40 mv. This represents

[illegible]

(8) *John, the president of the company, is a very good person.*

[illegible]

It was suggested by the committee that the following be included in the report of the committee on the subject of the proposed amendment to the constitution of the American Medical Association.

a potential difference of a magnitude in the vicinity of 100mv. On the basis of a proposed sodium shift mechanism or a marked increase in the membrane permeability to the sodium ion during the active period, there exists a possible mode of operation. At this point we consider the theoretical aspects of the dynamics of ionic motion as a basis for determining this potential shift.

We assume initially that the concentration of the sodium ion in the interstitial fluid is at a higher value than that in the axoplasm. Extensive investigation has permitted this assumption in our development. (58) If we may further consider only the cation Na and exclude the anions, we postulate that the Na ion is subjected to the action of two forces, one a diffusion force and the other an electric force. We define the mobility u of the cation as the velocity in cm/sec of an ion under a fall of potential of 1 volt per cm. (57) The potential gradient dV/dx is, of course, the change in potential per increment dx , where V , the potential is defined as the work required to move a positive charge from infinity to the reference point in question against the electric field forces exerted by an arbitrary charge q considered to be concentrated at a point r from the reference point in question where the potential is calculated.

The potential at point A, therefore, is expressed as:

$$\text{Eq. (VII)} \quad V_A = - \int_V^A \frac{\rho}{er^2} dvdr = -Q/er_A$$

where ρ is the positive charge density per unit volume.

If a cation were free to move under a potential gradient, its velocity v_c would be: $v_c = u \nabla V / dx$ where u is defined as the velocity in cm. per sec. if an ion under a gradient of one volt per cm. The negative sign signifies motion in the direction of decreasing potential.

We previously defined \bar{E} as the electric field force acting on a unit charge and equal to Q/er^2 and since $\bar{E} = - \nabla V / dx$, ⁽⁹⁾ the force acting on a mole of cations is:

$$F_1 = F_c \nabla V / dx$$

where F_c equals 96,500 coulombs per chemical equivalent. The force F_1 will be expressed in terms of volt-coulombs per cm. per mole of univalent cations.

We may express the ratio of the ionic velocity v_c to the absolute value of the electric force per mole F_1 which ratio may be written as u/F_c . When any other force is applied, the product of this ratio and the applied force will equal the resultant velocity of the mole of cations, ⁽¹⁴⁾ assuming that the resistive force function is the same in each instance.

Consider a thin element of volume ΔV where Δ may represent 1 cm³ of surface area of the nerve membrane and

The probability of finding a molecule in a certain state is given by

$$P_i = \frac{e^{-\epsilon_i/kT}}{\sum_j e^{-\epsilon_j/kT}}$$

where ϵ_i is the energy of the i th state and k is Boltzmann's constant.

If a system is in thermal contact with a reservoir at temperature T , the probability of finding it in a certain state is given by

$$P_i = \frac{e^{-\epsilon_i/kT}}{\sum_j e^{-\epsilon_j/kT}}$$

where ϵ_i is the energy of the i th state and k is Boltzmann's constant.

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dx , an increment of thickness. It is further assumed that in view of the physical concentrations of sodium, that an osmotic pressure gradient exists in the same direction as the electric force field.

The osmotic pressure gradient is $-dP/dx$ while the Einstein relation for the diffusion force is adP . This latter force should be equal and opposite to the force required to prevent osmosis. (14) In the volume considered let c be the concentration in moles per cc. The diffusion force is exerted on $cadx$ moles of cations and the diffusion force per mole is then $-dP/cdx$.

Providing Van't Hoff's Law can be applied in the case of physiological solutions, the partial osmotic pressure due to the Na ions, $P = RTc$ and thus $dP/dx = RTdc/dx$ where R and T have their usual significance. Thus the osmotic force per mole is $-RT/c \times dc/dx$. We then calculate the velocity component due to the osmotic force as:

$$(v_c)_o = -u/F \cdot RT/c \cdot dc/dx$$

Thus the actual velocity of the cations must be the sum of the velocities due to the electrical osmotic forces:

$$v_c = -u dV/dx - uRT/Fc \cdot dc/dx$$

Now the number of moles of ions passing through a surface, n , is a function of velocity, concentration, area and time. This is expressed as:

$$dn = -uadt (cdV/dx + RT/F \cdot dc/dx)$$

By a proper conversion, the preceding equation becomes an expression for the ionic current density for the Na ions.

Eq. (VIII)

$$I_{Na} = (F/a) da/dt = -u (Ve dV/dx + RT da/dx)$$

which equation is identical with the equation developed (43) by Goldman in his treatment.

This equation implies that the diffusion and the electric field forces should establish an ionic current. The equation as it stands could be used to determine the potential across the membrane providing the necessary boundary conditions were known. One difficulty here is the determination of the membrane thickness, the investigation of which is still in the early stages. (44) From a knowledge of the gradient and the thickness, the potential difference would be simple to calculate.

It was noted by this writer, in his review of the literature, that the membrane capacitance was reported not to change appreciably during activity. (42) If we accept this idea of a constant capacitance we have in effect a simple means to check the magnitude of the potential which is due to a transfer of sodium ions.

By means of the usual relationship, $C = Q/V$, we have by direct differentiation, rearrangement, and integration the relation

$$\text{Eq. (IX-a)} \quad V = 1/C \int_{Q_2}^{Q_1} dq = (Q_1 - Q_2)/C$$

where $(Q_1 - Q_2)$ equals the charge transported by the sodium ions.

of a first approximation, the preceding results are
 sufficient for the present purpose for the time being.

(1911)

$$x = \frac{1}{2} \left(\frac{1}{\sqrt{1-\beta^2}} + \frac{1}{\sqrt{1+\beta^2}} \right) + \frac{1}{2} \left(\frac{1}{\sqrt{1-\beta^2}} - \frac{1}{\sqrt{1+\beta^2}} \right)$$

which is identical with the results obtained
 by Johnson in his treatment.

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It has been shown by this method, in the case of the

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$$x = \frac{1}{2} \left(\frac{1}{\sqrt{1-\beta^2}} + \frac{1}{\sqrt{1+\beta^2}} \right) + \frac{1}{2} \left(\frac{1}{\sqrt{1-\beta^2}} - \frac{1}{\sqrt{1+\beta^2}} \right)$$

which is identical with the results obtained by the method of the oblique field

the ions during the period of the rise of the action potential. A period of 0.456 mil. sec and a membrane capacitance of 1.2 micro farads/cm² was used in these calculations, based on values from Hodgkins and Latz. (47) The expression for the potential as a function of the ionic current and capacitance is finally expressed as:

Eq. (IX-b)

$$V = \frac{(\text{Ions}/t_1 - t_2)/\text{cm}^2 / 4.85 \times 10^{10} \text{ ions/coul.}}{1.2 \mu\text{F}/\text{cm}^2}$$

In a second consideration we may draw an analogy to a series resistance capacitance circuit. The literature gives a membrane resistance of approximately 1200 ohms per cm² in the resting state. Both Curtis and Cole (42) state that a membrane resistance change occurs with activity. However, on the basis of the work Curtis and Cole did, this writer disagrees that this is a resistance change but a total impedance change due to a variation in the frequency of the current of stimulation which was employed. From a consideration of alternating current theory this is readily understood since in a series or parallel resistance capacitive circuit, the impedance will decrease with an increase in the frequency. The writer tends to take the view expressed by Rober (59) that the plasma membrane offers a great resistance to flow of electrolytes. The writer postulates therefore that the ionic flow shall be regarded in a d.c. sense with a minimum membrane re-

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istance of 1200 ohms/cm².

Consider a condenser in series with a pure resistance element R where the capacitance has a value of 1.5×10^{-6} farads/cm² and R equal to 1200 ohms/cm². We desire to determine the voltage required to discharge the circuit in 0.456 millisece when a given charge is transferred. This relationship is readily developed from a consideration of the well known equation:

$$I = dq/dt = (V/R)e^{-t/RC}$$

and upon integration within the limits of t_1 and t_0 , the results:

$$Q = -CV_0 \left[e^{-t_1/RC} - e^{-t_0/RC} \right]$$

or,

$$Q = CV(1 - e^{-t_1/RC})$$

and the voltage required will be:

$$\text{Eq. (IX-e)} \quad V = Q/C(1 - e^{-t_1/RC})$$

When proper substitution has been made with a value of t_1 equal to 4.56×10^{-4} seconds, the equivalent of the rise time of the action potential, with the aforementioned R and C values, the following relationship governs:

$$V = 3.705Q/C$$

(C) Computations

The required Q value in both cases may be readily evaluated by the following method. The procedure which was followed in the laboratory for the determination of the

distance of 1000 miles.

Consider a problem in which a gas is contained in a cylinder of length l and cross-sectional area A . The gas is at a pressure p and has a temperature T . The gas is assumed to be an ideal gas. The gas is contained in a cylinder of length l and cross-sectional area A . The gas is at a pressure p and has a temperature T . The gas is assumed to be an ideal gas.

The total energy of the gas is

$$E = \frac{3}{2} N k T$$

and the total momentum is

$$P = \frac{1}{3} N m \bar{v}^2$$

$$P = \frac{1}{3} N m \bar{v}^2$$

and the total energy is

$$E = \frac{3}{2} N k T$$

then the total energy is

equal to the total energy of the gas.

then the total energy is

equal to the total energy of the gas.

$$E = \frac{3}{2} N k T$$

(c) Consider

the problem in which a gas is contained in a cylinder of length l and cross-sectional area A .

then the total energy is

equal to the total energy of the gas.

number of sodium ions which transit the membrane area of less than 1 per stimulus has been outlined in Section II. We now define the terms which will be used in the final expression for magnitude of the sodium transfer. Let

- $(dn/dt)_5$ the count rate of the stimulated nerve sample at time t_5 ,
- $(dn/dt)_6$ the count rate of the control nerve sample at time t_6 ,
- $(dn/dt)_7$ the count rate of 1 ml. of the radioactive bath solution at time of t_7 .

The time of reference shall be that time at which the stimulations of the nerve section were terminated for each experimental run and designated t_0 . Thus:

- $(t_1 - t_0)$ the time interval for determination of the decay factor, where l may take values 3, 6, 7.
- $a(t_1 - t_0)$ the correction factor for radioactive decay where a is the decay constant or probability factor. This value is multiplied into all count rates to compare them at the reference time t_0 .
- w^0 The wet weight of a control nerve section in mg.
- w^s The wet weight of a stimulated nerve section in mg.
- SA_f The total surface area of the nerve fibres in a nerve section. The product of the number of fibres, mean fibre diameter and section length. Thus,

$$SA_f = (\# \text{ fibres}) (\pi \bar{D} l)$$
- N_s The total number of stimuli delivered to the nerve section via the electrodes.

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For ease of handling in the equations we shall call the correction factor for the count rate for the stimulated nerve section f_1 ; for the control section f_2 , and the factor for the bath solution count rate f_3 .

$(Na)_{bs}$ The number of sodium ions present per ml. of bath solution.

The number of sodium ions adsorbed by the control section per mg of wet tissue is expressed as,

$$\text{Eq. (A)} \quad (Na)_{bs} \cdot (dn/dt)_s f_2 / (dn/dt)_7 \cdot f_3 \cdot v^c$$

While the number of sodium ions present in the stimulated nerve section upon completion of the run will be,

$$\text{Eq. (A1)} \quad (Na)_{bs} \cdot (dn/dt)_s \cdot f_1 / (dn/dt)_7 \cdot f_3$$

The number of sodium ions which are adsorbed on the surface of the stimulated section are assumed to be calculable on a weight basis. For nerves of comparable diameter such as the stimulated and control sections were in this case, this assumption is justified. Since, if we consider b as the volume density of nerve tissue, the weight of a nerve section is,

$$W = (b \pi r^2 l) = \left(\frac{W}{V} \cdot \pi r^2 l \right) = \pi \cdot \text{surface area}$$

and since the adsorption is a function of surface area exposed, all other factors acting equally, we may validly say that the adsorption of ions on the surface is in direct proportion to the weight of a nerve section. On this basis, the number of sodium ions adsorbed by the stimu-

lated nerve section may be expressed as:

$$\text{Eq. (III)} \quad (\text{Na})_{\text{DS}} \cdot (\text{dn/dt})_5 \cdot f_2 \cdot v^2 / (\text{dn/dt})_7 \cdot f_3 \cdot v$$

The final expression for the number of sodium ions which transit the nerve membrane per cm^2 per stimulus is as follows:

Eq. (XIII)

$$(\text{Na})_{\text{DS}} \cdot \left[(\text{dn/dt})_5 f_1 - (\text{dn/dt})_6 f_2 v^2 / v^0 \right] / (\text{dn/dt})_7 f_3 \Delta A_f$$

The data tabulated in Section VIII 3-2 was calculated on the basis of the foregoing relationship.

GENERAL CONSIDERATIONS

The question may well be raised as to the possible effect the beta and gamma radiation of the bathing solution has on the nerve section under stimulation, and might not that radiation be a factor pertinent to the results as observed and computed. This problem may be answered in consideration of two points. The first point is that a control nerve section was immersed with the section under stimulation for the same period of time and subjected to the same radiation dose. Any change in uptake, due to an increase in membrane permeability, would reflect itself in the control section as well as the stimulated nervous tissue. The second consideration is that with reference to the low degree of sensitivity of nerve tissue to any

$$E_{\alpha} \gamma_{\alpha\beta} (2\pi/\alpha) \delta^{\alpha\beta} \gamma_{\alpha\beta} \gamma_{\alpha\beta} (\alpha/\alpha) \gamma_{\alpha\beta} (\alpha/\alpha) \gamma_{\alpha\beta} (\alpha/\alpha) \quad (21.9) \quad \text{and}$$

The third experiment was the effect of the amount of the stimulus on the response. The results are shown in Table 1. The response was significantly higher for the 100% stimulus than for the 50% stimulus. The response was also significantly higher for the 100% stimulus than for the 25% stimulus. The response was not significantly different for the 50% and 25% stimuli.

$$\gamma_{\mu\nu}(\partial/\partial x^\mu)(\partial/\partial x^\nu) \left[\frac{1}{2} \left(\frac{1}{\sqrt{g}} \frac{\delta S}{\delta g^{\mu\nu}} \right) - \frac{1}{2} \left(\frac{1}{\sqrt{g}} \frac{\delta S}{\delta g^{\mu\nu}} \right) \right] = 0 \quad (2.12)$$

and as the basis of the following investigation.

The committee was well informed as to the progress

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and no other (see, e.g., [10]).

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1. The first step is to identify the problem or question that needs to be answered. This involves understanding the context and the specific requirements of the task.

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Source: *Journal of the American Statistical Association*, 1997, Vol. 92, No. 439, pp. 1092-1103.

to the law system at consistently 95 percent since 1990

form of radiation, particulate or electromagnetic. As evidence of this we refer to the work of Dr. M. A. Rothenberg on permeability changes in nervous tissue as a result of irradiation with X-rays. He found that at a dose of 50,000 roentgens there was no statistical significance between the uptake of control and experimental tissue. He had to increase the dose to 125,000 R. before there was any statistical significance between the control and the experimental sections.⁽⁵⁰⁾ When these doses are compared to the maximum upper limit value which was computed in Section II, there is little reason to believe that the radiation had any significant effect on the permeability characteristics of the nerve tissue or any resultant effect on the results which have been attained.

From an analysis of the computed and observed results of this experiment, the initial point of inquiry is fairly well established. There is little doubt that a sodium ion transfer takes place during the nerve conduction process. With each sodium ion we have an associated charge and on consideration of the time factor involved, it follows that a current exists.

The point might be considered as to the barrier effect which the myelin sheath might exert on this ionic transfer and in particular, in this case where multi-fibered nerve was employed, the barrier effect of the connective tissue matrix between bundles in a trunk and in addition the en-

peroneous of the fibre bundles. In this regard, Fong and
 (61) Au believe on the basis of their investigations that
 connective tissue does present an effective diffusion
 barrier to an ion migration. However, Lorente de No
 (12) states with no reservations.

"It is difficult to believe that the connective tissue sheath of frog or bull frog nerve could act as an effective diffusion barrier that would delay for any period of time the penetration of ions into the nerve."

When one considers the ionic radius of the Na ion, which is approximately 0.95 \AA , and the clearances of the stream of connective tissue which may well be hundreds of times larger, one is inclined to agree with deNo. However, judging purely on the geometrical considerations, there is bound to exist a partial barrier to penetration no matter how slight.

With reference to the membrane surrounding the fibre, the situation is slightly modified. Schmitt and
 (62,63) Palmer have investigated the nerve sheath by means of X-ray diffraction studies, the findings of which bear on our problem. The sheath is believed to be composed of layers of mixed lipids wrapped in a concentric manner about the axoplasm or central cylinder. It is believed that protein elements alternate with lipid micelles layer for layer, and that the protein and lipid is in a micelle form with a definite orientation in a radial direction. The equatorial spacing is said to be on the

order of 17 Å and the meridional spacing is about 5 Å. On a purely geometrical consideration, disregarding a charge on the membrane, an atom of sodium should have little difficulty transiting the membrane with about the same ease as a baseball going through an open window. The thickness of this nerve membrane will, of course, vary with size but the literature often quotes the thickness in the range of 100-170 Å.

It will be recalled from Section I, that until the year 1940, the magnitude of the resting potential was thought to limit the magnitude of the action or spike potential. It was believed, and this portion of the theory is still considered valid, that the concentration of internal and external potassium was responsible for the resting potential, the magnitude of which, for most studies, was reported in the vicinity of 60mv. The polarity of the potential was such that the membrane was positive with reference to the internal axoplasm in the resting state. As shown in diagram A-1 of the Appendix, on Activity, the membrane not only goes to zero, it passes through and assumes a negative potential with respect to the inner core. This phase shift leaves us with some 100 mv to account for. This is quite evident by inspection of a reproduction of the spike potential which Curtis and Cole observed in the squid single fibre giant axon internal and external set up.

The idea of Potassium leakage from a fibre has been

reported by many observers through the years. This is in support of the membrane hypothesis as we defined it. In addition, changes in the Potassium concentration in the external bath solution of the nerve has resulted in a marked decrease of the magnitude of the action potential with an increase in the external Potassium concentration. However, with the phase reversal and the magnitude of the action potential to be considered the original membrane hypothesis fails.

The reversal of the membrane potential can be explained on the basis of the Sodium hypothesis as advanced (47) by Hodgkin and Katz. It is assumed that in the resting state, the nerve membrane is selectively permeable to the potassium and not to the Sodium ion. During activity, this selective permeability shifts with the membrane becoming permeable to the sodium. They support their hypothesis in light of experimentation wherein by a variation of the external bath solution concentration of sodium, the height of the action potential was proportionately affected. When isotonic solutions containing a decreased sodium concentration were applied it was found that solutions of less than 50% of the normal sodium concentration caused the magnitude of the reversed potential to be zero. Likewise, the height of the action potential was increased by an increase of the sodium concentration above the normal. From the results of their work, it is indicative that the

Sodium shift hypothesis has a good foundation.

The experimental phase of this research supports the work of Hodgkins and Huxley in that a definite ionic transfer was noted. However, in the problem of correlating the magnitude of that transfer it was necessary to draw the parallel in electrical circuitry, following Cole's lead. (46)

It is fully realized that any explanation of this type is certainly not unique nor should it ever be so considered in biological experimentation. It will be noted in Tables I and II and in the summary of computed data of the Appendix, that there is some force function, perhaps not fully nor completely defined by our equations nor understanding, at work within certain time limitations. The writer agrees with Cole to the extent that when the problem is transferred into physical theory of electrical circuits we have at least a technique for mathematical analysis.

In our case we first applied the idea of a membrane of pure capacitance and negligible resistance. It was noted from the computed values that the answer was not here in magnitude at least. When we considered the resistance capacitance circuit, the magnitude of the computed values came closer to that desired magnitude.

The point might well be raised as to why the writer made the assumption that the Sodium transfer was specific to certain time limits such as the rise time of the action

The Department of the Interior has been advised that the Bureau of Land Management is in the process of reviewing the status of the various lands owned by the United States in the State of California. It is requested that you advise the Bureau of the results of your investigation.

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The United States will be pleased to see the progress made in the investigation of the activities of the Communist Party in the United States.

potential. The answer can be had on the basis of Hodgkins and Katz's work. Our objective was to show a magnitude correlation in view of the assumption that an ionic current does flow during the rise time period. The writer had to make this assumption for computational purposes. However, on the basis of the membrane theory it does logically follow that this transfer would be a function of time. When Hodgkins and Katz showed the dependence of the magnitude of the potential reversal on the concentration of the Sodium in the bathing solution, it followed that an agent acted during the period from the zero potential value to the maximum of the negative swing, the time which is called by the improper term "rise" time.

The exact nature of the mechanism of action of the membrane selectivity is not too well known and is in consequence, the subject of much speculation. Danielli and (65) others have treated this matter in great detail. There is no doubt in this writer's mind that metabolic function enters into the picture at this point. Many factors point to this, such as the effect of low oxygen content in vicinity of an active nerve. As a result, the action potential and conduction velocity fall far from normal. In addition, there is the work of Shanes et al (68) which shows an adverse effect on the resting membrane potential when the nerve is bathed in a solution containing metabolic inhibitors.

[illegible]

It has been noted earlier, as shown by curves 5-2(a) and (b), that there is a reversal of the sodium shift mechanism after a certain period of time. In the case of the nerve sections from the subject group of *Rana pipiens* this occurred at 33'20", and in the second group *Rana catesbiana* the results show a decreased uptake and a lowering of the ionic current flow after 18'40". It may be pointed out that the only two cases of zero uptake or negative flow were computed from data from runs of 50' stimulation time. It is evident from the results that the uptake and ionic current falls after a certain period of time. Perhaps the concentration gradient suffers a significant change during long periods of stimulation or possibly the metabolism of the nerve is suffering from an unbalance due to a disproportion of ions. However difficult to describe, some force is operating and a reverse sodium shift is apparent after a certain time.

If we considered the possibility of a membrane inductance element as was proposed some time ago by Cole, in order for the relationship,

$$L \frac{di}{dt} + Ri + q/C = 0$$

to apply to a situation of a non oscillatory case, it would require a parameter relationship of the following nature. Where R/L would be greater in magnitude than $2/(LC)^{\frac{1}{2}}$. By selecting various values of membrane resistance which we might consider, for a capacitance value of

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1.2×10^{-6} farads/cm², we would have the following inductance requirements.

Resistance in ohms/cm ²	Inductance in millihenries
1000	100mH
500	75.8mH
25	.187mH

However, the idea of a membrane inductance element is not too plausible in view of the constituents of the membrane.

At the present time, Curtiss and Cole treat the mechanism of conduction on the basis of the circuit analogy. Referring to Diagram A-3 of the appendix, it is imagined that the nerve cell membrane is composed of a series of circuit elements as shown. During the resting phase all condensers are at the same potential and there is no current flow. When for any reason, the membrane permeability, which is the "resistance" of the electrical circuit, and the emf of unit "A" changes, then the condenser in this unit will discharge. The adjacent condenser will discharge through the external and internal resistances. This will repeat itself all along the nerve fibre resulting in a conducted impulse. Both Curtiss and Cole depend on the metabolic function to restore the membrane to its resting state in the same manner as we mentioned earlier.

In closing the discussion it may be said that the findings of this work support the hypothesis of Hodgkins and Hata with reference to the Sodium shift and its correl-

ation with the magnitude of the potential of action. While the values of the computed potentials arising from the analogy drawn on the basis of a resistance capacitance circuit do not approach the required 100 mv magnitude, there is a strong inference that a parastrophically similar biophysical phenomenon is functioning.

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CHAPTER V SUMMARY AND CONCLUSIONS

Theoretical considerations predict the existence of an ionic current across a permeable membrane which separates two unequal distributions of the same cation, as a result of the action of a diffusion force and an electric field force.

The inadequacy of the Bernstein membrane theory of the nerve conduction process has been corrected by a modification advanced by Hodgkins and Katz to explain the phase reversal and the magnitude of the action potential of the nerve. The resting nerve is held to be selectively permeable to potassium ions and impermeable to the sodium ion. During the activity, it is believed that this selective permeability of the nerve membrane shifts to favor the sodium ion. The modification provides a reversed membrane potential on the basis of this sodium shift, providing the external concentration of sodium is greater than the internal concentration.

The object of this study was to investigate the existence of a sodium transfer across the nerve membrane of a modified nerve during the conduction process and to further correlate the magnitude of this ionic current and that of the associated action potential taking into consideration accepted values of the membrane parameters of resistance and capacitance.

THE HISTORY OF THE UNITED STATES

The history of the United States is a story of the growth of a nation from a small colony to a great power. It is a story of the struggles of the people to establish a government of their own, and of the triumphs of the American spirit. The story begins with the first settlers, who came to the New World in search of a better life. They found a land of opportunity, but also a land of hardship. They fought for their freedom, and they won. They built a nation that has stood the test of time, and that has inspired the people of the world.

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The multifiber sciatic nerve trunks of two separate subject groups were used for this study, 10 adult leopard frogs (*Rana pipiens*) and 10 adult bull frogs (*Rana catesbeiana*). The usual radioactive tracer techniques were employed in the determination of the amount of sodium taken up by nerve sections, utilizing the isotope ^{24}Na in isotonic acid-blooded Ringer's solution. Nerves were stimulated at a rate of 100 per second for three different time intervals. Normal control sections were used and separate surface adsorption studies were made for resting sections of both subject groups on the basis of the time of immersion.

The results attained by the experimental study were:

1. A positive uptake of sodium per mg. of wet tissue was determined for 24 of the 28 cases under study. The uptake was linear with respect to time in the range from zero to 33'30". After the 33'30" period a reverse shift was noted with a marked decrease in uptake. The two negative results fell in the 33' range.

2. The number of moles of sodium entering the section per stimulus averaged 1.772×10^{-10} moles/stimulus/cm² during the 0-33'30" time interval. On the basis of a rate of entry per second during the rise-time period, 5.31×10^{-11} moles of sodium traversed the membrane/cm²/sec.

3. The existence of an ionic current was shown to exist in 24 out of 28 cases under study. In the first

subject group, in the interval from 0-35'20", this current averaged 0.0076 mA./cm^2 .

4. When the membrane is considered as a simple condenser circuit with negligible resistance, the average potential difference, computed on a charge capacitance relationship for the first subject group in the time interval from 0-35'20", is 14.27mv.

5. When the membrane circuit is considered as a resistance capacitance setup in series, the average potential difference, computed on a resistance capacitance and time basis, is for the first subject group 55.97 mv.

On the basis of this experimental work, the following conclusions are reached:

1. An ionic current does exist across the membrane of the nerve fibre during the conduction process as predicted by Hodgkins and Katz.

2. The rate of entry as determined by these investigations was calculated to be 2×10^{-11} moles of Na./cm²/sec during the rise period. This is in agreement within a factor of 4 with the theoretical value of 6.4×10^{-11} moles/cm²/sec as computed by Hodgkins and Katz.

3. While the potential considerations of a membrane resistance capacitance circuit yield only a potential value of 55.97mv., only half that required to account for the magnitude of the negative portion of the action or spike potential, it is felt that a parametrically similar

biophysical system is in operation.

4. From the data obtained, there is an indication of a sodium shift reversal after a certain stimulation time and period of nervous activity.

All points considered, these findings support the proposed modification to the membrane theory as advanced by Hodgkins and Katz.

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69.	Security, 1971	Security, 1971	Security, 1971
70.	Security, 1971	Security, 1971	Security, 1971

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The number and character of the persons who are subject to the provisions of the Act are as follows:

1. Persons who are

2. Persons who are

3. Persons who are

4. Persons who are

5. Persons who are

6. Persons who are

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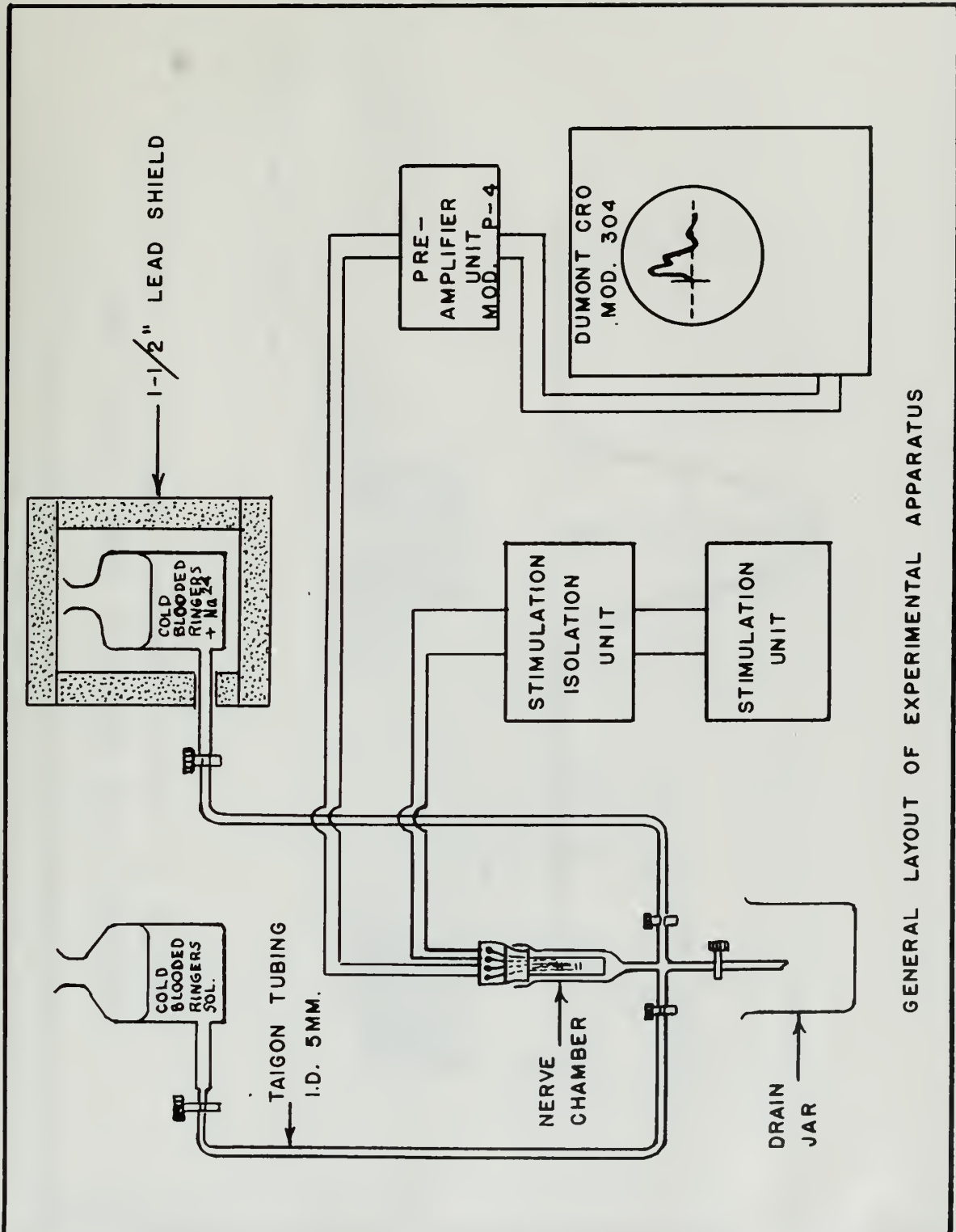
18. Persons who are

19. Persons who are

20. Persons who are

21. Persons who are

SECTION VII. APPENDIX



GENERAL LAYOUT OF EXPERIMENTAL APPARATUS

DIAGRAM A-1

PROPAGATION OF AN IMPULSE IN SINGLE NERVE FIBRE,
 ACCORDING TO MODIFIED MEMBRANE HYPOTHESIS. GLASSER (47)

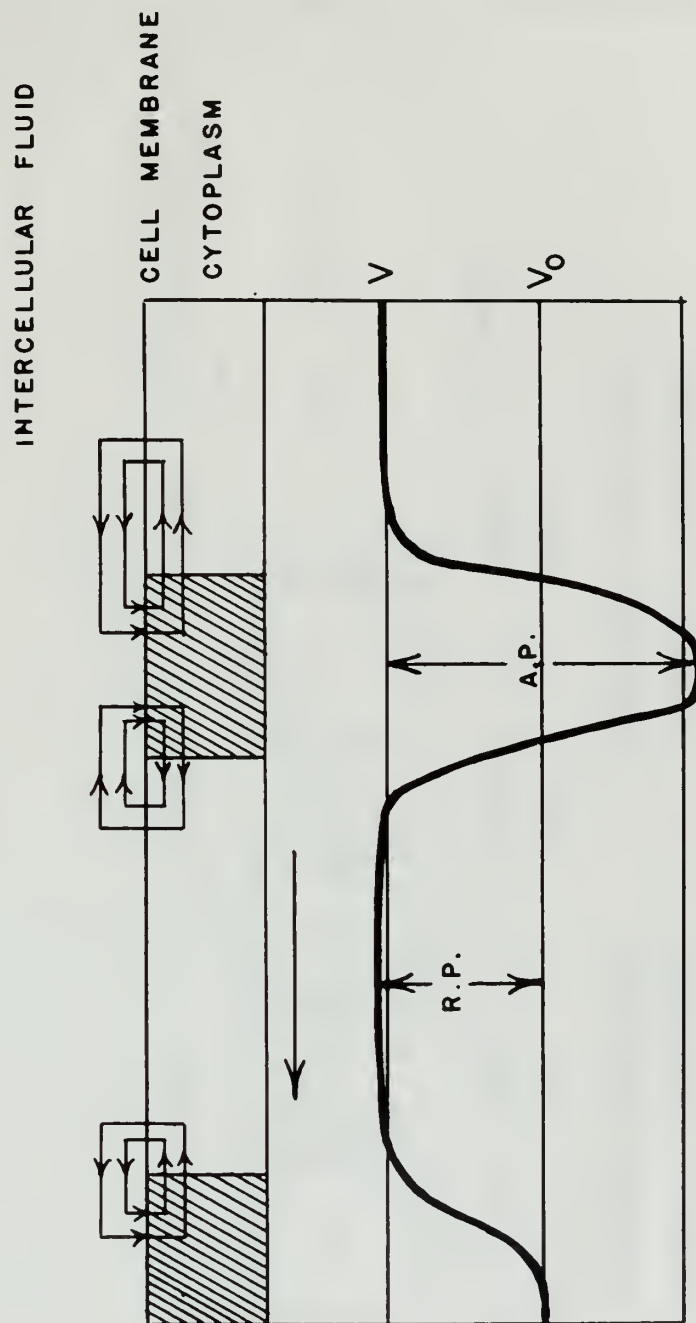


DIAGRAM A-2

CIRCUIT DIAGRAM OF A SINGLE NERVE FIBRE: CURTIS & COLE (46)

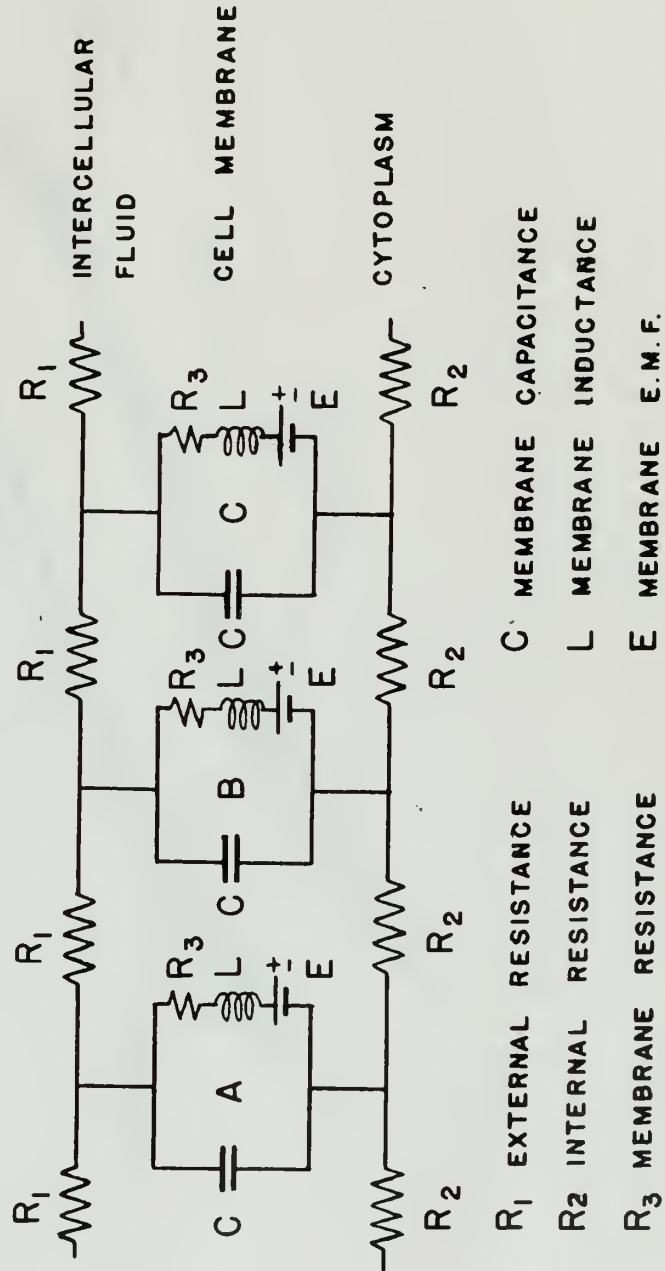


DIAGRAM A-3

LONGITUDINAL SECTION OF MYELINATED NERVE FIBRE - HISTOLOGY,
LEWIS & BREWER. REF. (45)

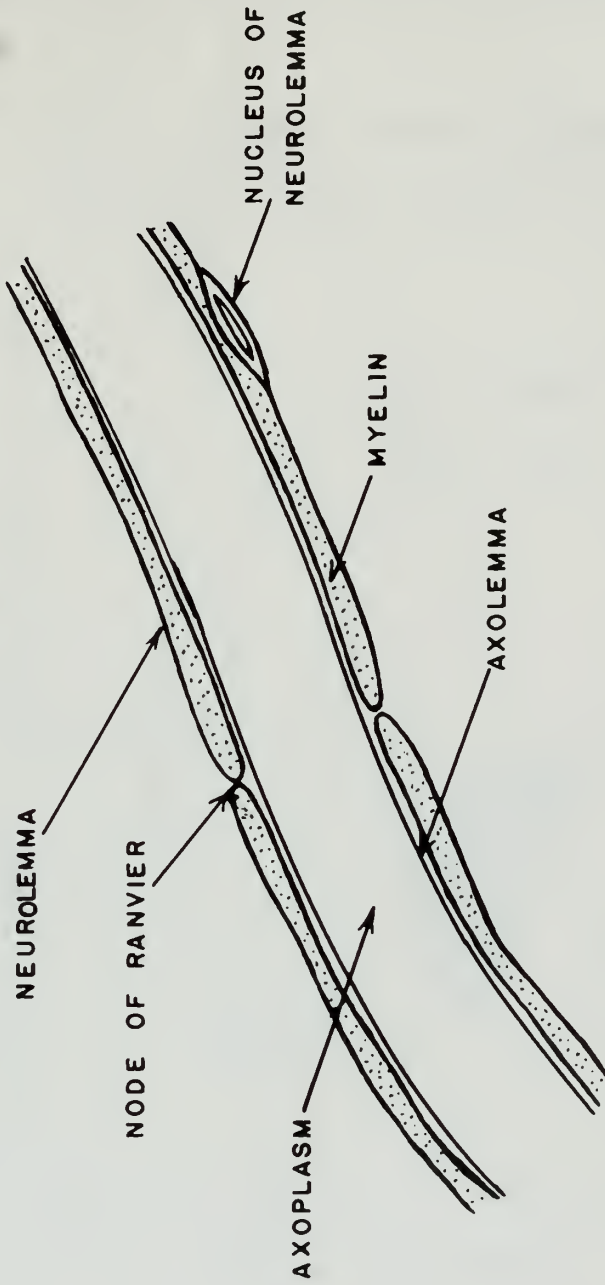


DIAGRAM A-4

TYPICAL ACTION POTENTIAL OBSERVED
ON STIMULATION OF MULTIFIBRED NERVE
(SCIATIC) OF RANA PIPIENS

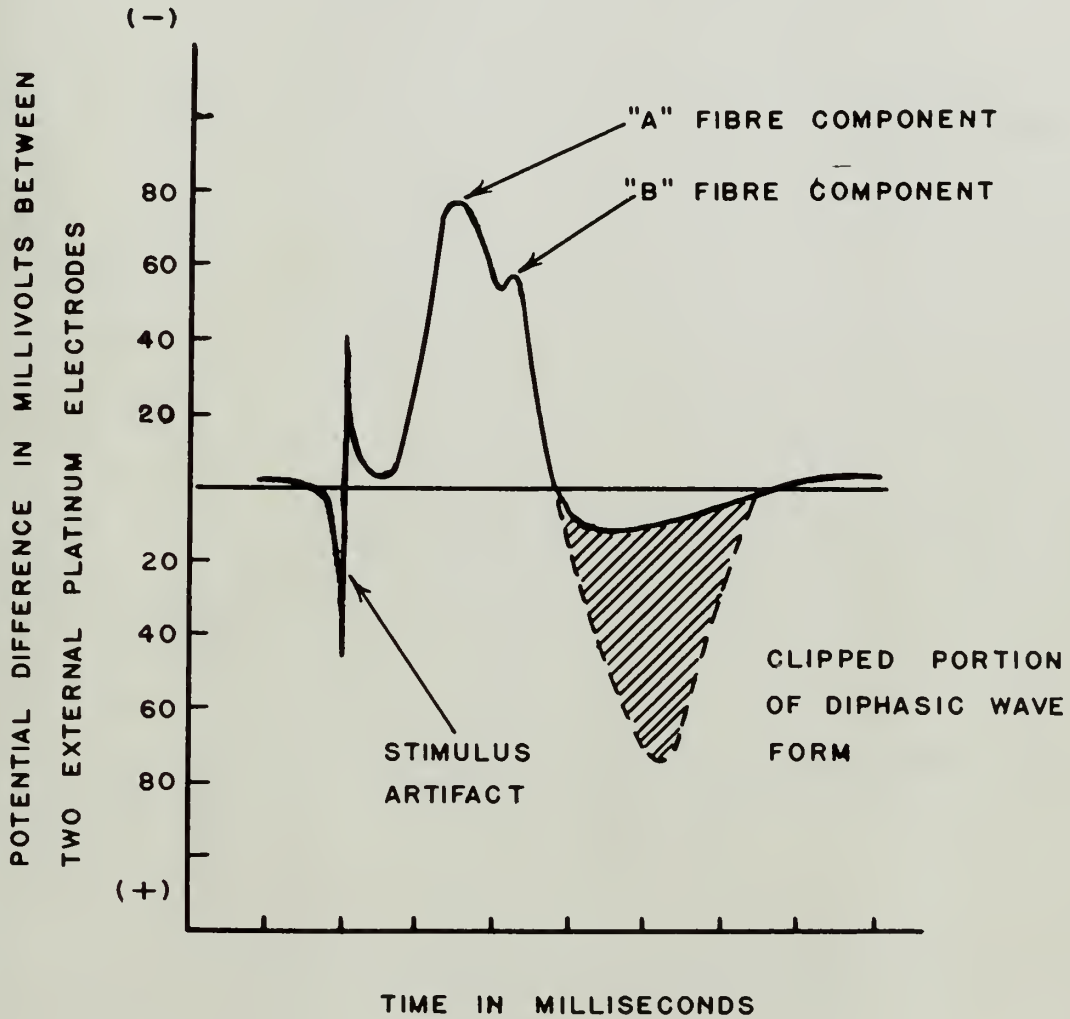


DIAGRAM A-5

ACTION POTENTIAL OF SINGLE NERVE FIBRE
GIANT SQUID AXON: FROM CURTIS & COLE (13)

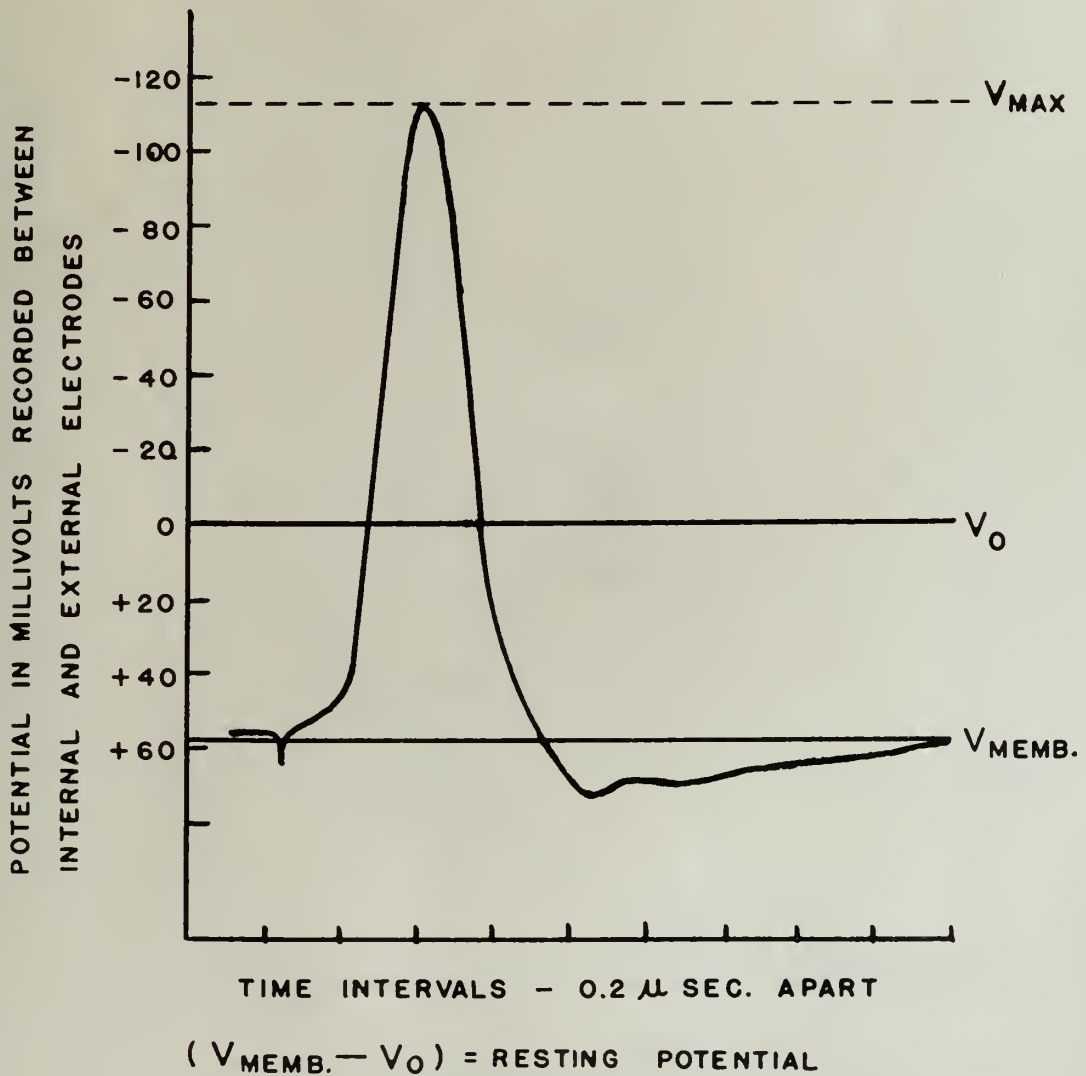
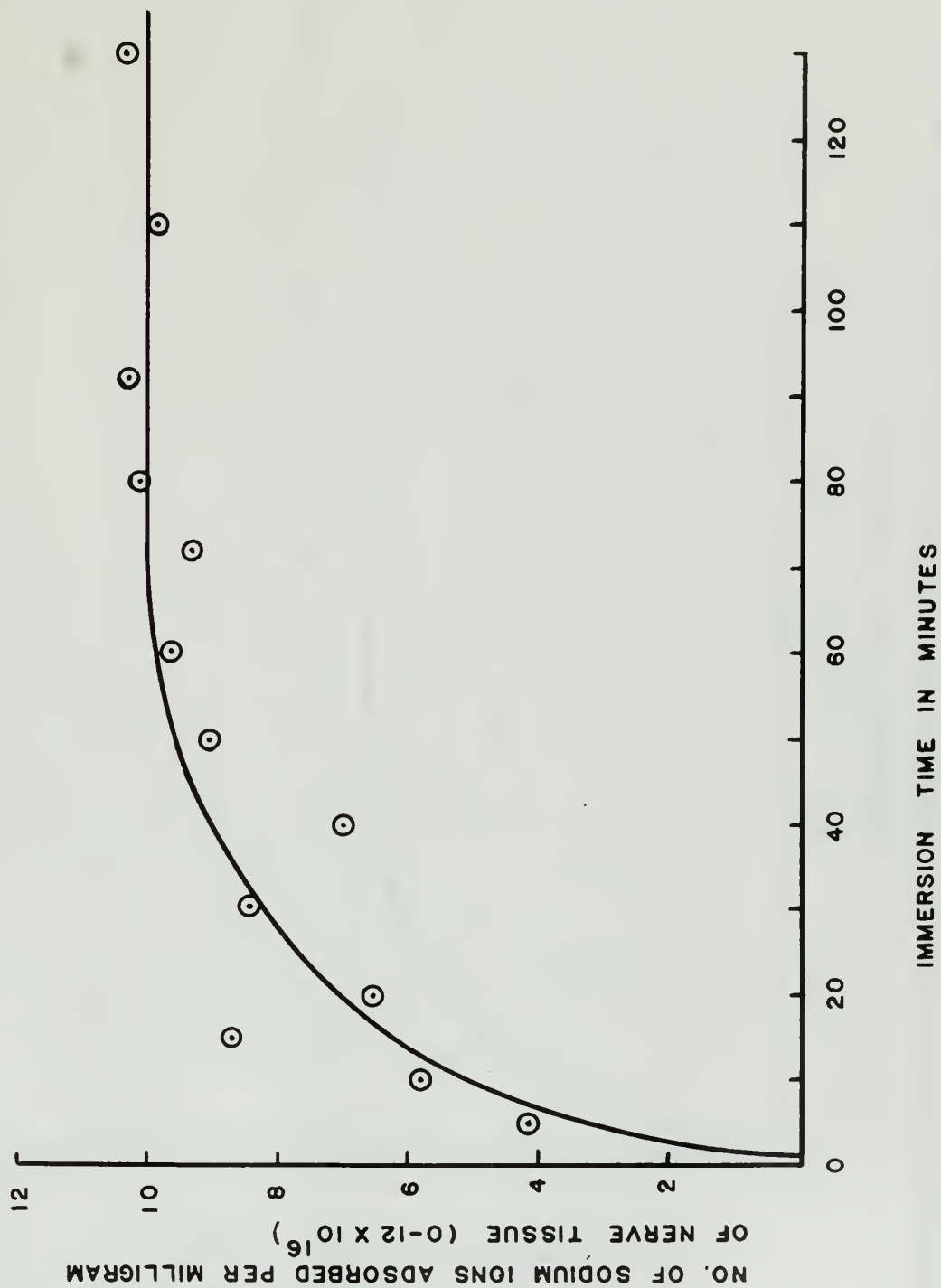


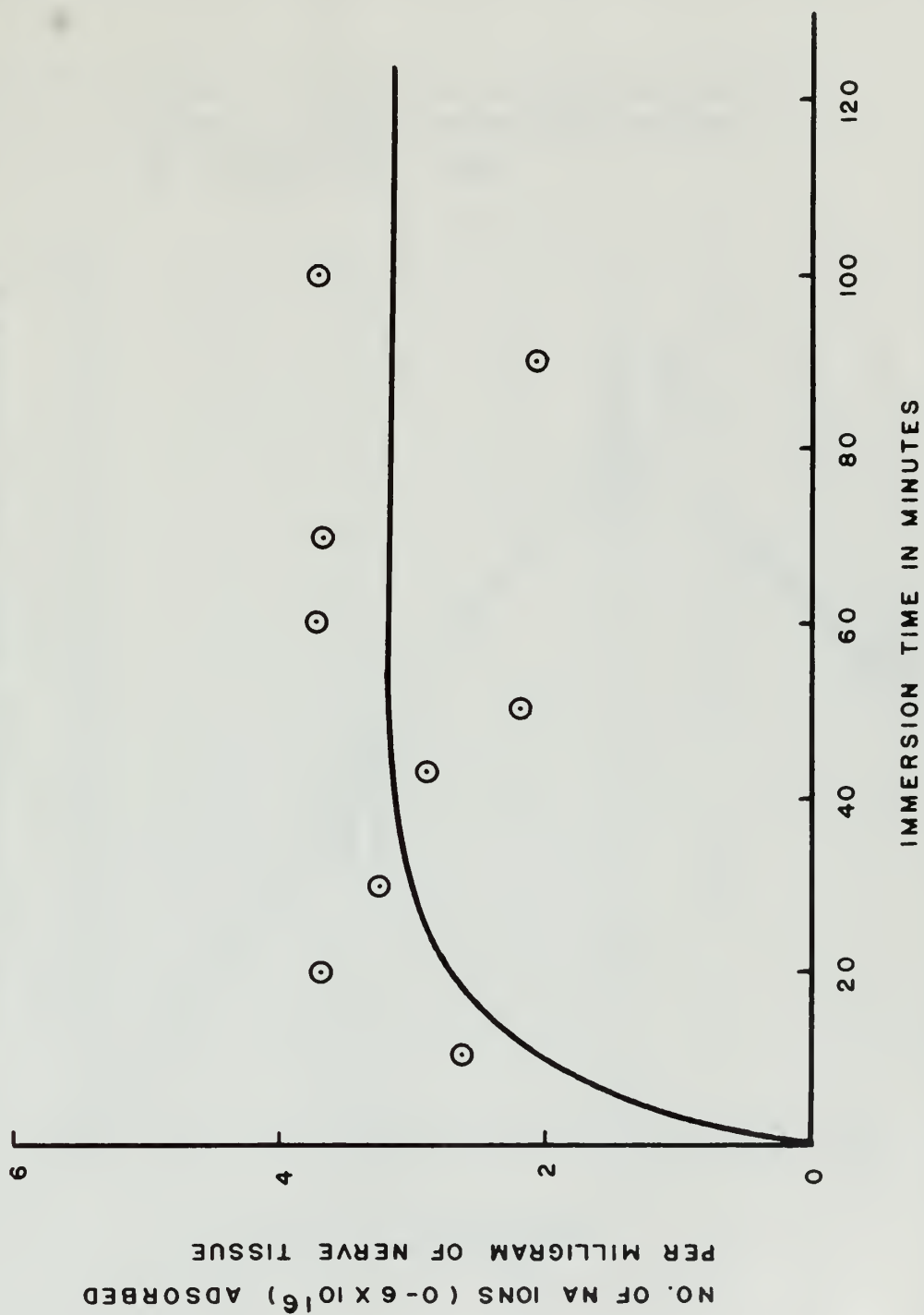
DIAGRAM A-6

SURFACE ADSORPTION OF SODIUM VS. IMMERSION
TIME FOR NERVE SECTION (SCIATIC - RANA PIPIENS)



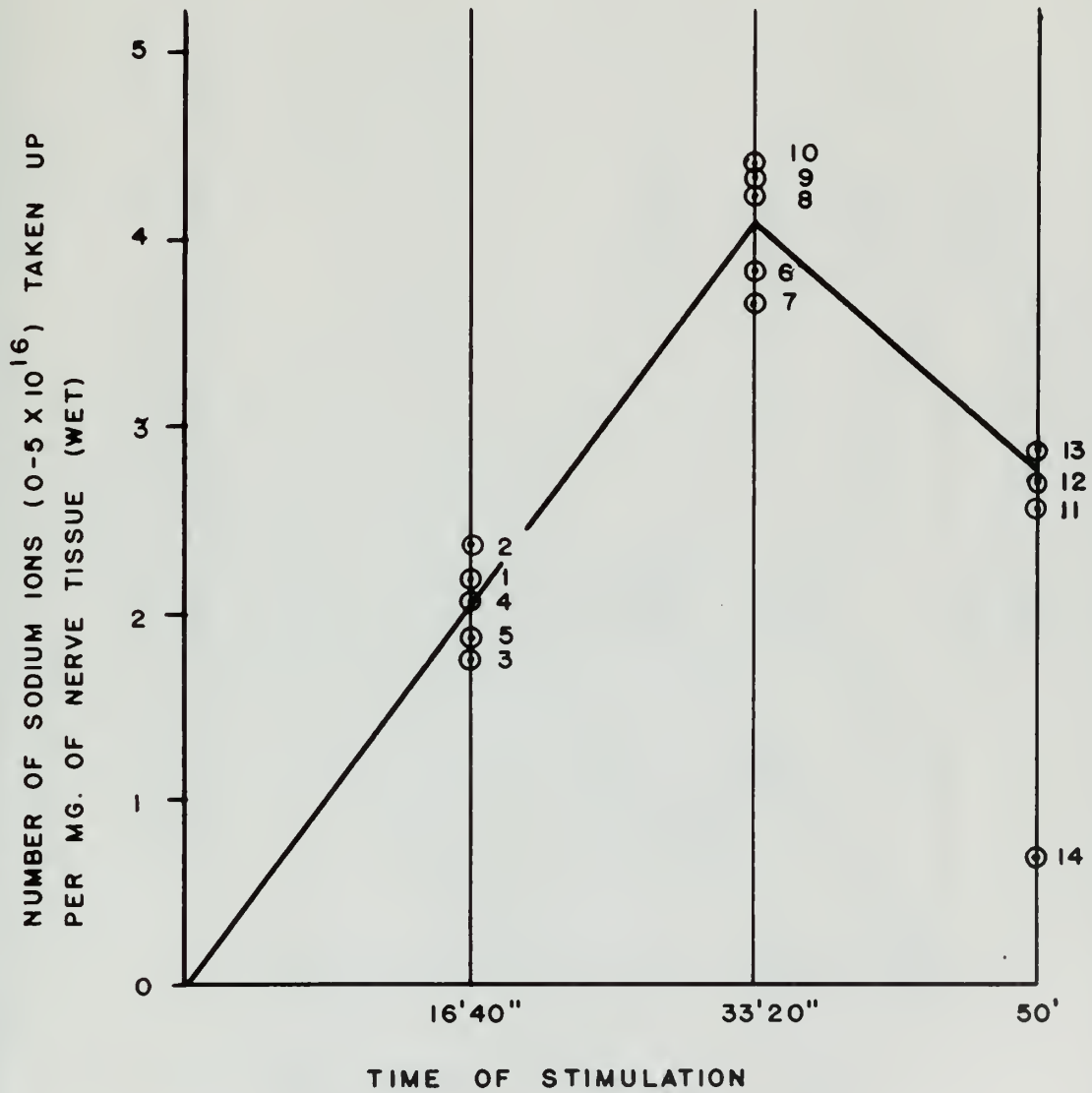
GRAPH NO. B-1 (a)

SURFACE ADSORPTION OF SODIUM VS. IMMERSION TIME
FOR NERVE SECTION (SCIATIC - RANA CATESBIANA)



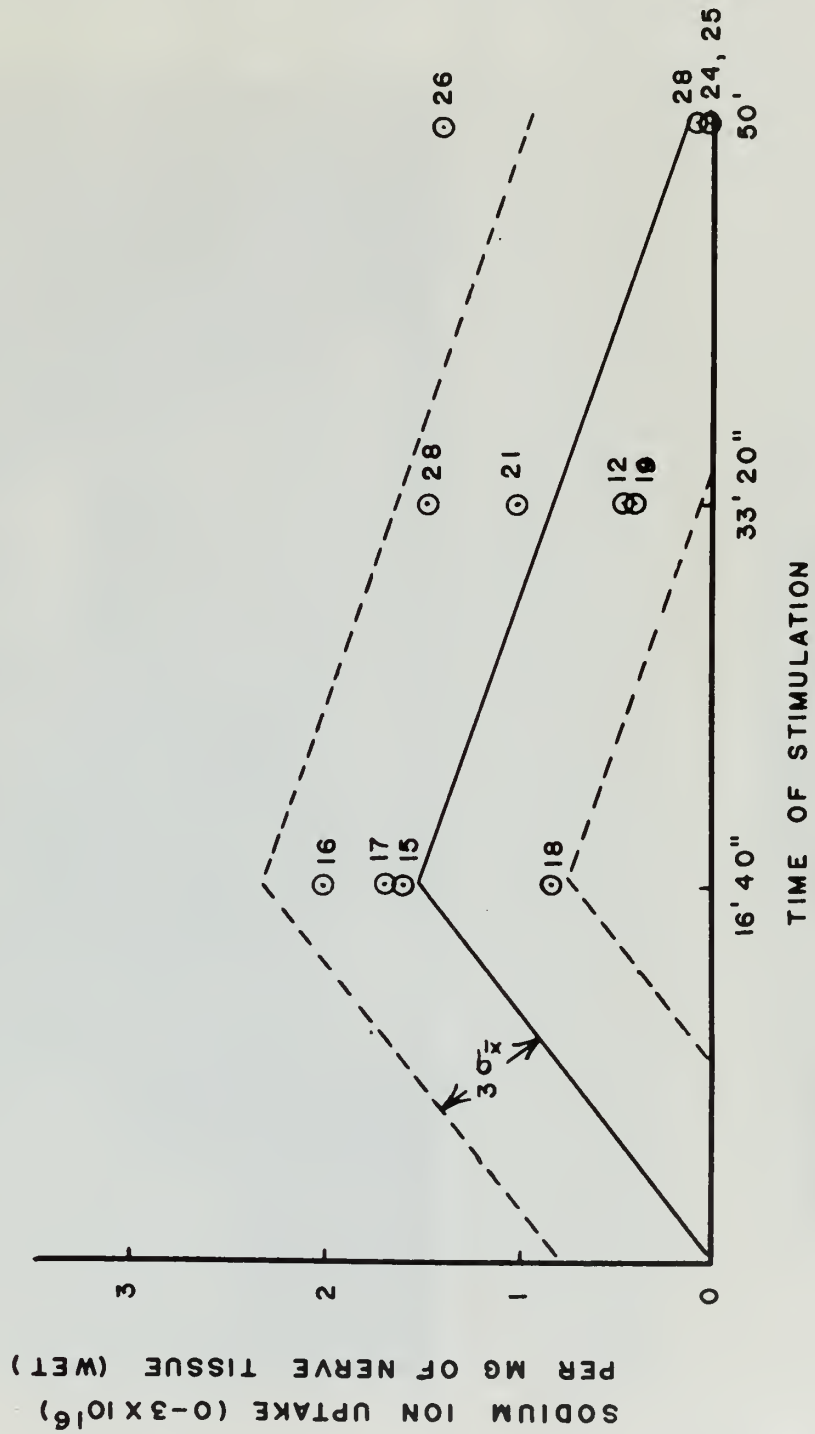
GRAPH NO. B-1 (b)

UPTAKE OF SODIUM BY MULTIFIBRED NERVE
SECTION (SCIATIC FROM RANA PIPIENS)
VS. STIMULATION TIME

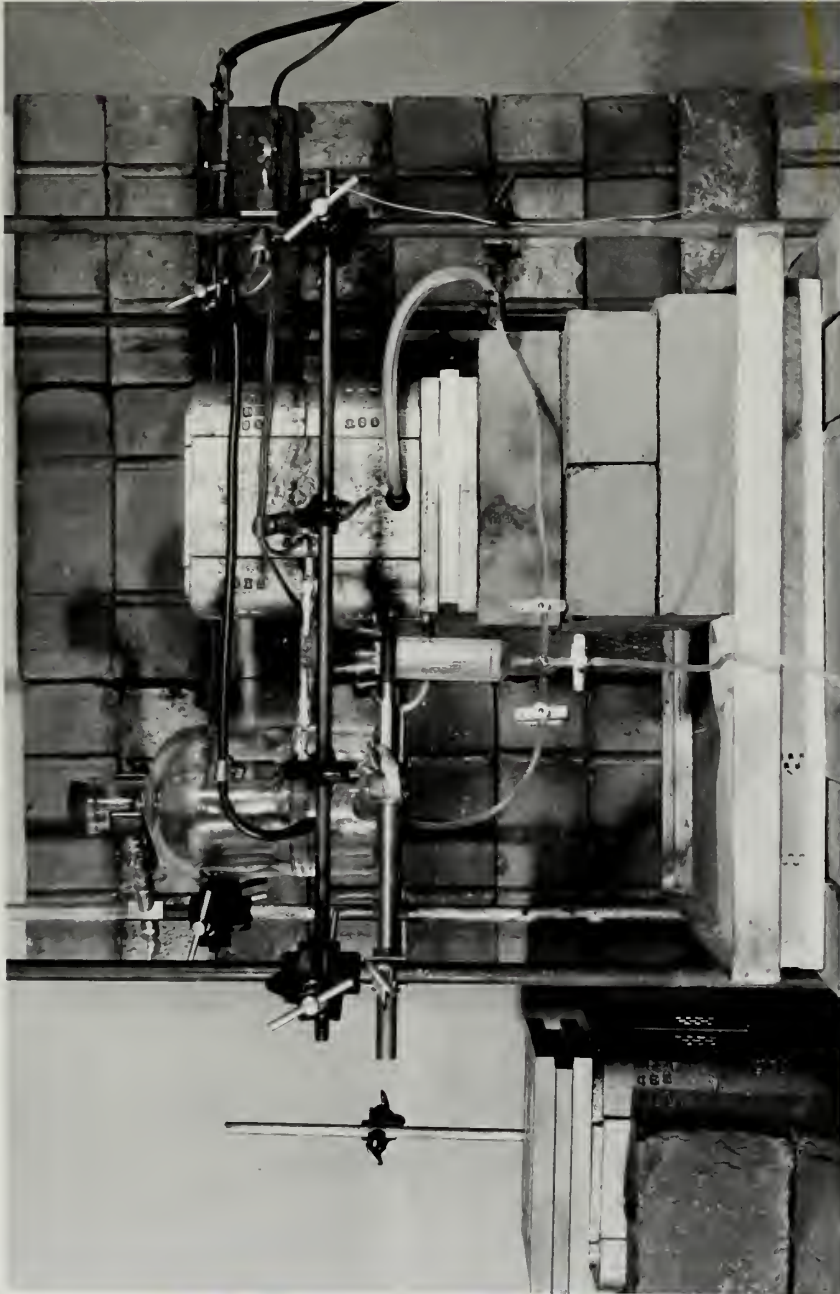


GRAPH NO. B-2 (a)

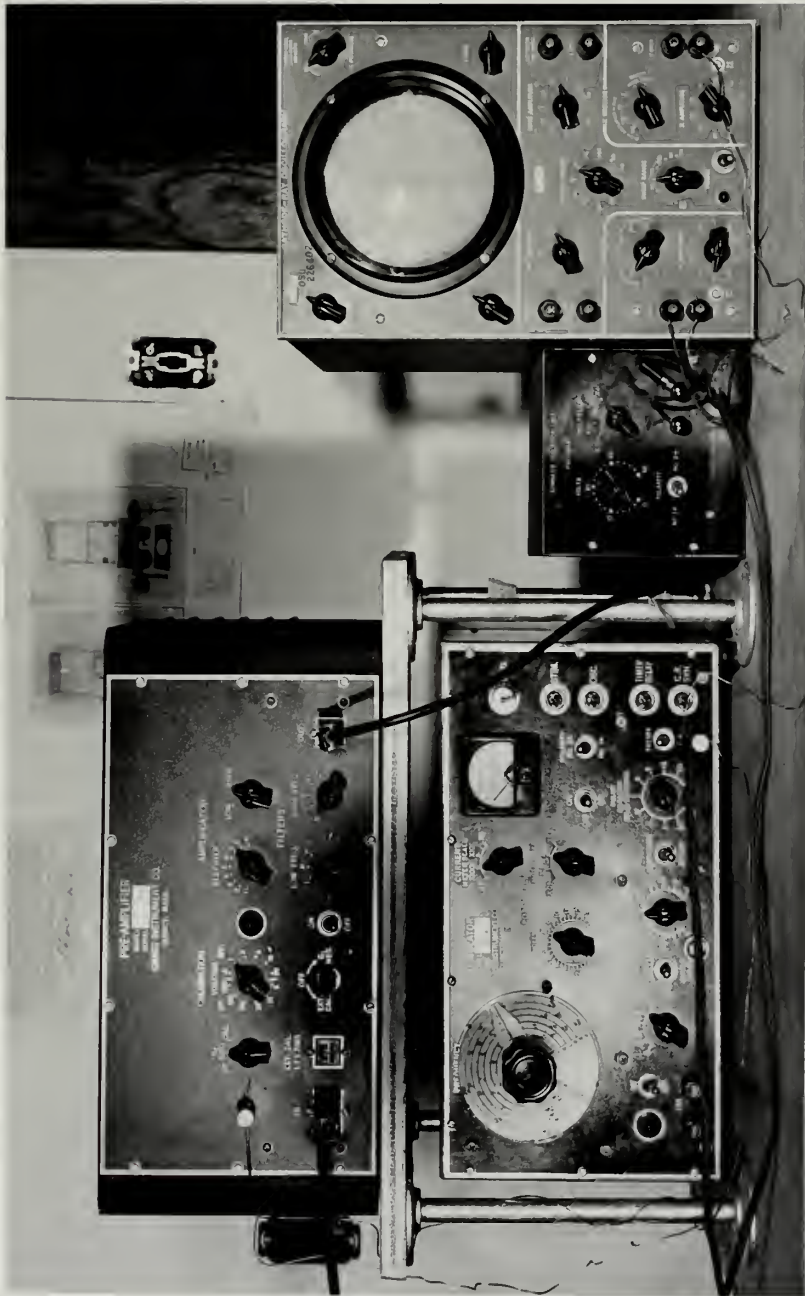
UPTAKE OF SODIUM BY MULTIFIBRED NERVE SECTION
(SCIATIC OF RANA CATESBIANA) VS. STIMULATION TIME



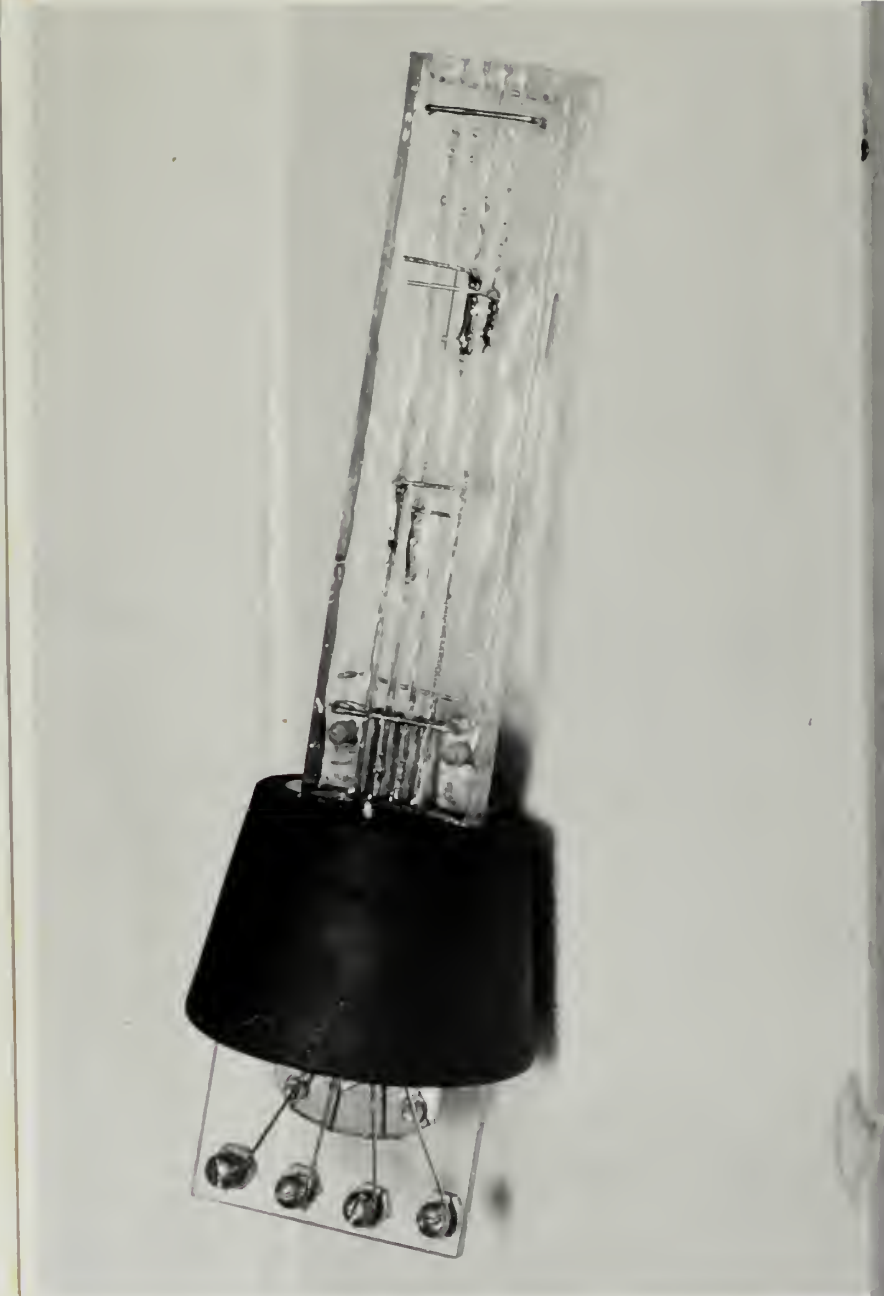
GRAPH NO. B-2 (b)



PHOTOGRAPH C-1: THE NERVE STIMULATION UNIT,
SHIELDING AND ASSOCIATED EQUIPMENT



PHOTOGRAPH C-2: THE ELECTRONIC STIMULATING,
AMPLIFYING AND RECORDING EQUIPMENT



PHOTOGRAPH C-3: THE NERVE STIMULATION PLATFORM

D. PROTOCOLS

The individual data observed and computed are summarized in the following tables. The Roman type numerals appearing in parentheses under the column headings refer to that similarly indexed equation in Section II by means of which the particular column value was computed.

Runs numbered 1 to 14 were made on nerve sections excised from the common leopard frog, *Rana pipiens*, while runs numbered from 15 to 25 were sections from the giant bull frog, *Rana catesbeiana*. All subjects appeared in a healthy state, manifesting full reflexes, prior to sacrifice. All experimental nerve sections were stimulated prior to and on the completion of a run to determine if the capacity to conduct an impulse was still retained. This action was monitored by the appearance of the action potential appearing on the oscilloscope screen.

RUN NO.	EXPERIMENTAL COMMENT
1-3, 12-14	Stimulated at frequency of 100 per sec. Time run 12'40", for a total number of stimuli delivered of 100,000
5-10, 15-20	Stimulated at a frequency of 10 per sec. Time run 22'20", for a total number of stimuli delivered of 200,000
11-14, 21-25	Stimulated at a frequency of 100 per sec. Time run 20', for a total number of stimuli delivered of 100,000.

APPENDIX I

The following data were received and reported by the
 in the following order: The same type material ap-
 pearing in parentheses under the column heading refers to
 that similarly labeled material in Section II of Volume 10
 which the particular column refers was omitted.

Item numbered 1 to 15 were made in 1935 and
 related from the same source (see page 15). All
 items numbered from 16 to 25 were made from the same
 self from same materials. All subjects appeared in a
 family state, manifesting full normalcy, before the
 item. All experimental nerve sections were performed
 before the end of the duration of a run to determine if
 the exposure to alcohol as indicated was still possible.
 This section was included in the exposure of the same
 potential appearing in the following table.

ITEM NO.	EXPERIMENTAL DATA
1-15, 16-25	Estimated as 100% for a total exposure of alcohol delivered at 100,000
1-15, 16-25	Estimated as a percentage of the per cent. of alcohol delivered total amount of alcohol delivered at 100,000
1-15, 16-25	Estimated as a percentage of the per cent. of alcohol delivered total amount of alcohol delivered at 100,000

TABLE I

Run number	1	2	3	4	5
Date	3/5/51	3/9/51	3/21/51	3/2/51	3/22/51
Weight of control in mg.	9.8	11.4	15.5	13.5	15.2
Length of control in mm.	19	25.	24	27	31
Weight of stim. sec. mg.	11.0	9.6	14.4	11.8	14.0
Length of stim. sec. mm.	24	29.5	25	23	28
Vol. of bath sol. in ml.	12.75	12.5	14.3	13.5	14.2
$(dn/dt)_5$	6.01	7.80	14.05	9.02	13.2
$(dn/dt)_6$	3.69	6.45	11.5	8.22	14.2
$(dn/dt)_7$	307.0	844	951	928	890
$t_5 - t_0$ (min.)	95	62	59	115	99
$t_6 - t_0$	83	53	48	102	26
$t_7 - t_0$	56	44	30	96	32
f_1 -decay factor	1.075	1.048	1.05	1.095	1.03

[illegible]

TABLE I-(CONT'D)

Run Number	1	2	3	4	5
f_2 -decay factor	1.065	1.043	1.0309	1.000	1.080
f_2 - "	1.043	1.0349	1.0383	1.0762	1.125
$(dn/dt)_5 f_1$	5.70	8.15	14.68	9.82	16.7
$(dn/dt)_6 f_2$	3.93	3.72	11.95	8.77	14.43
$(dn/dt)_7 f_3$	950	875	936	995	911.5
Na ions in bath Col/ml	9.49×10^{19}	7.91×10^{19}	7.015×10^{19}	7.015×10^{19}	7.615×10^{19}
Ratio of Na-ions to $(dn/dt)_7 f_3$	9.93×10^{15}	9.04×10^{16}	7.12×10^{16}	7.04×10^{16}	7.7×10^{16}
Na ions adsorbed by control per sq. cm	4.01×10^{16}	5.34×10^{16}	5.47×10^{16}	3.84×10^{16}	7.42×10^{16}
Na ions present stim. nerve sect. refer to XII	6.77×10^{17}	7.18×10^{17}	10.42×10^{17}	6.92×10^{17}	13.0×10^{17}
Na ions adsorbed stim. nerve sect. refer to XII	4.41×10^{17}	5.115×10^{17}	7.87×10^{17}	4.5×10^{17}	10.12×10^{17}
Na ions taken up by section.	2.15×10^{17}	2.55×10^{17}	2.55×10^{17}	2.42×10^{17}	5.55×10^{17}
Total surface area of fibres cm ²	2.83	29.3	14.85	2.9	27.85

1	2	3	4	5	6	7	8
01	01	01	01	01	01	01	01
02	02	02	02	02	02	02	02
03	03	03	03	03	03	03	03
04	04	04	04	04	04	04	04
05	05	05	05	05	05	05	05
06	06	06	06	06	06	06	06
07	07	07	07	07	07	07	07
08	08	08	08	08	08	08	08
09	09	09	09	09	09	09	09
10	10	10	10	10	10	10	10
11	11	11	11	11	11	11	11
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54	54	54	54	54	54	54	54
55	55	55	55	55	55	55	55
56	56	56	56	56	56	56	56
57	57	57	57	57	57	57	57

TABLE I-(continued)

no number	1	2	3	4	5
Na ions taken up by section per stimulus	12 2.36x10	12 2.25x10	12 2.55x10	12 2.42x10	12 2.32x10
Na ions taken up by section /stimulus/cm	2.04x10	10 7.88x10	10 10.27x10	10 11.55x10	10 9.41x10
moles of Na taken up by sect. /stimulus/cm	-12 1.45x10	-12 1.47x10	-12 1.70x10	-12 1.75x10	-12 1.53x10
Na ions taken up by sect./sec/cm ²	12 10.65x10	12 10.33x10	12 20.24x10	12 21.12x10	12 18.82x10
moles of Na taken up by sect. /sec/cm ²	-10 2.51x10	-10 2.55x10	-10 2.41x10	-10 2.21x10	-10 2.15x10
seoulorda transferred/C.450sec/cm.	-8 1.25x10	-8 1.22x10	-8 1.64x10	-8 1.66x10	-8 1.50x10
Potential diff.in mv., pure capacit-ive case (eq. IX-5)	12.5	10.26	12.82	14.79	12.53
Potential diff.in 49.2 mv., capacitance and resistance (eq. IX-6)	49.2	33.0	60.2	33.2	45.6

1

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TABLE I-(CONT'D)

Run Number	6	7	8	9	10
Date	3/9/51	3/10/51	3/10/51	3/10/51	3/2/51
Weight of control in mg.	17.7	8.2	16.2	17.8	18.2
Length of control in cm.	17	19	20	27	25
Weight of alk. sect. -g	17.6	8.1	15.4	10.8	13.9
Length of alk. sect. -cm.	21	18	20	25	22.5
Volume of bath sol. in ml.	11.2	11.25	11.4	11.4	11.4
(dn/dt) ₅	9.55	7.90	12.49	9.25	19.04
(dn/dt) ₆	.27	4.19	7.23	9.93	14.27
(dn/dt) ₇	750	1015	691	461	11.14
t ₅ -t ₀ (min)	86	169	26	35	258
t ₆ -t ₀ "	81	158	19	35	219
t ₇ -t ₀ "	55	57	29	22	43
f ₁ -decay factor	1.068	1.157	1.019	1.017	1.195

Speed (km/h)	Time	3-7/15	7-10/15	10-15/15	15-20/15
1-2/15	20	10	10	10	10
2-3/15	30	100	70	70	100
3-4/15	40	105	80	100	100
4-5/15	50	105	100	100	100
5-6/15	60	105	100	100	100
6-7/15	70	105	100	100	100
7-8/15	80	105	100	100	100
8-9/15	90	105	100	100	100
9-10/15	100	105	100	100	100
10-11/15	110	105	100	100	100
11-12/15	120	105	100	100	100
12-13/15	130	105	100	100	100
13-14/15	140	105	100	100	100
14-15/15	150	105	100	100	100
15-16/15	160	105	100	100	100
16-17/15	170	105	100	100	100
17-18/15	180	105	100	100	100
18-19/15	190	105	100	100	100
19-20/15	200	105	100	100	100
20-21/15	210	105	100	100	100
21-22/15	220	105	100	100	100
22-23/15	230	105	100	100	100
23-24/15	240	105	100	100	100
24-25/15	250	105	100	100	100
25-26/15	260	105	100	100	100
26-27/15	270	105	100	100	100
27-28/15	280	105	100	100	100
28-29/15	290	105	100	100	100
29-30/15	300	105	100	100	100
30-31/15	310	105	100	100	100
31-32/15	320	105	100	100	100
32-33/15	330	105	100	100	100
33-34/15	340	105	100	100	100
34-35/15	350	105	100	100	100
35-36/15	360	105	100	100	100
36-37/15	370	105	100	100	100
37-38/15	380	105	100	100	100
38-39/15	390	105	100	100	100
39-40/15	400	105	100	100	100
40-41/15	410	105	100	100	100
41-42/15	420	105	100	100	100
42-43/15	430	105	100	100	100
43-44/15	440	105	100	100	100
44-45/15	450	105	100	100	100
45-46/15	460	105	100	100	100
46-47/15	470	105	100	100	100
47-48/15	480	105	100	100	100
48-49/15	490	105	100	100	100
49-50/15	500	105	100	100	100
50-51/15	510	105	100	100	100
51-52/15	520	105	100	100	100
52-53/15	530	105	100	100	100
53-54/15	540	105	100	100	100
54-55/15	550	105	100	100	100
55-56/15	560	105	100	100	100
56-57/15	570	105	100	100	100
57-58/15	580	105	100	100	100
58-59/15	590	105	100	100	100
59-60/15	600	105	100	100	100
60-61/15	610	105	100	100	100
61-62/15	620	105	100	100	100
62-63/15	630	105	100	100	100
63-64/15	640	105	100	100	100
64-65/15	650	105	100	100	100
65-66/15	660	105	100	100	100
66-67/15	670	105	100	100	100
67-68/15	680	105	100	100	100
68-69/15	690	105	100	100	100
69-70/15	700	105	100	100	100
70-71/15	710	105	100	100	100
71-72/15	720	105	100	100	100
72-73/15	730	105	100	100	100
73-74/15	740	105	100	100	100
74-75/15	750	105	100	100	100
75-76/15	760	105	100	100	100
76-77/15	770	105	100	100	100
77-78/15	780	105	100	100	100
78-79/15	790	105	100	100	100
79-80/15	800	105	100	100	100
80-81/15	810	105	100	100	100
81-82/15	820	105	100	100	100
82-83/15	830	105	100	100	100
83-84/15	840	105	100	100	100
84-85/15	850	105	100	100	100
85-86/15	860	105	100	100	100
86-87/15	870	105	100	100	100
87-88/15	880	105	100	100	100
88-89/15	890	105	100	100	100
89-90/15	900	105	100	100	100
90-91/15	910	105	100	100	100
91-92/15	920	105	100	100	100
92-93/15	930	105	100	100	100
93-94/15	940	105	100	100	100
94-95/15	950	105	100	100	100
95-96/15	960	105	100	100	100
96-97/15	970	105	100	100	100
97-98/15	980	105	100	100	100
98-99/15	990	105	100	100	100
99-100/15	1000	105	100	100	100

Source: 2-10-10-10-10

TABLE I-(CONT'D.)

Run Number	6	7	8	9	10
f_2 -decay factor	1.056	1.1285	1.015	1.025	1.110
f_3 - "	1.051	1.0446	1.023	1.0245	1.013
$(dn/dt)/\eta f_1$	10.20	7.77	12.71	8.60	27.80
$(dn/dt)/\eta f_2$	3.43	4.525	7.65	10.20	13.32
$(dn/dt)/\eta f_3$	7.00	10.30	6.97	673	1174
Na ions in with sel. el.	7.55x10 ¹⁹	7.85x10 ¹⁹	9.55x10 ¹⁹	9.25x10 ¹⁹	8.25x10 ¹⁹
Ratio of Na. conc. to $(dn/dt)/\eta f_1$	10.0x10 ¹⁶	9.71x10 ¹⁶	12.55x10 ¹⁶	13.65x10 ¹⁶	8.6x10 ¹⁶
Na. ions adsorbed by control per sq.	1.971x10 ¹⁶	4.65x10 ¹⁶	9.45x10 ¹⁶	7.85x10 ¹⁶	7.9x10 ¹⁶
Na. ions present stim. nerve sect.	10.21x10 ¹⁷	6.94x10 ¹⁷	14.92x10 ¹⁷	13.87x10 ¹⁷	13.85x10 ¹⁷
Na. ions adsorbed stim. nerve sect. after eq. 111	6.47x10 ¹⁷	2.99x10 ¹⁷	10.23x10 ¹⁷	8.44x10 ¹⁷	12.4x10 ¹⁷
Na. ions taken up by section.	1.74x10 ¹⁷	2.945x10 ¹⁷	6.54x10 ¹⁷	4.65x10 ¹⁷	8.90x10 ¹⁷
Total surface area of fibres cal.	21.85	17.20	29.85	24.85	22.4

TABLE I-(CONT'D)

Run Number	6	7	8	9	10
Na ions taken up by section per stimulus	12 2.37x10	12 1.47x10	12 3.87x10	12 2.21x10	12 1.45x10
Na ions taken up by section / stimulus/cm	10 15.4x10	10 8.24x10	10 10.94x10	10 9.2x10	10 15.4x10
Holes of Na taken up by sect. / stimulus/cm	-13 2.55x10	-13 1.57x10	-13 1.02x10	-13 1.21x10	-13 2.25x10
Na ions taken up by sect. / sec/cm	-13 20.2x10	12 14.48x10	13 21.73x10	12 15.8x10	13 30.2x10
Holes of Na taken up by sect. / sec/cm	-10 5.12x10	-10 3.74x10	-10 3.24x10	-10 3.33x10	-10 5.12x10
Aluminum cross-sectioned/0.456mm ² /sec	-3 2.445x10	-3 1.219x10	-3 1.75x10	-3 1.437x10	-3 2.435x10
Potential diff. in sec. Pure capacit- 175 case (Eq. 11-3)	20.55	11.0	14.5	12.4	20.55
Potential diff. in sec. Capacit- 175 case and resistance (Eq. 11-3)	75.1	40.5	54.2	45.9	75.1

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WASHINGTON, D. C.
OFFICE OF THE SECRETARY
GENERAL INVESTIGATIVE DIVISION
WASHINGTON, D. C.
7-12-51

TABLE 1-(CONT'D)

Run Number	11	12	13	14
Date	1-20-51	1-21-51	1-21-51	1-21-51
Weight of control in mg.	13.2	14.4	13.4	23.5
Length of control in mm.	21	24	23	29
Weight of stim. cont. mg.	14.6	12.6	13.2	20.2
Length of stim. cont. mm.	25	23	23.2	34
Volume of bath sol. in ml.	13.0	12.8	12.7	13.1
$(dm/dt)_0$	61.3	54.4	14.55	3.54
$(dm/dt)_6$	62.4	21.3	10.75	5.17
$(dm/dt)_{17}$	1049.9	1169	989	800.2
t_0-t_6 (min.)	46	70	253	53
t_6-t_0 (min.)	43	62	240	53
t_7-t_0 (min.)	23	46	16	11
f_1 decay factor	1.278	1.0549	1.2104	1.037

TABLE I--(CONT'D)

Run number	11	12	13	14
f_2 -test factor	1.0000	1.0000	1.0000	1.0000
f_3 + "	1.0000	1.0000	1.0000	1.0000
$(m/ct)g^2_1$	0.00	0.00	0.00	0.00
$(m/ct)g^2_2$	0.00	0.00	0.00	0.00
$(m/ct)g^2_3$	0.00	0.00	0.00	0.00
Na loss in data set 1/51.	0.00x10 ¹⁰	0.00x10 ¹⁰	0.00x10 ¹⁰	0.00x10 ¹⁰
Ratio of an conc. to (m/ct)g ² ₁	0.00x10 ¹⁰	0.00x10 ¹⁰	0.00x10 ¹⁰	0.00x10 ¹⁰
Na loss absorbed by control per wt.	0.00x10 ¹⁷	0.00x10 ¹⁷	0.00x10 ¹⁷	0.00x10 ¹⁷
Na loss present after 1st test.	0.00x10 ¹⁰	0.00x10 ¹⁰	0.00x10 ¹⁰	0.00x10 ¹⁰
Na loss present after 2nd test.	0.00x10 ¹⁰	0.00x10 ¹⁰	0.00x10 ¹⁰	0.00x10 ¹⁰
Na loss taken up by section	0.00x10 ¹⁷	0.00x10 ¹⁷	0.00x10 ¹⁷	0.00x10 ¹⁷
Total surface area of fl. 1/51 in sec.	0.00	0.00	0.00	0.00

TABLE 1- (Cont'd)

Box Number	11	12	13	14
100 lbs. taken up by section per stimulus	1.10x10 ⁻¹²	1.13x10 ⁻¹²	1.06x10 ⁻¹²	1.12x10 ⁻¹²
100 lbs. taken up by section /stimulus/cm ²	4.44x10 ⁻¹⁰	4.37x10 ⁻¹⁰	4.44x10 ⁻¹⁰	3.0x10 ⁻¹⁰
Weight of 20 taken up by sect. /stim./cm ²	0.804x10 ⁻¹³	0.726x10 ⁻¹³	0.82x10 ⁻¹³	0.59x10 ⁻¹³
100 lbs. taken up by sect./sec/cm ²	10.8x10 ⁻¹⁵	8.8x10 ⁻¹⁵	10.8x10 ⁻¹⁵	7.65x10 ⁻¹⁵
Moles of H ⁺ taken up by sect. /sec/cm ²	1.74x10 ⁻¹⁰	1.37x10 ⁻¹⁰	1.9x10 ⁻¹⁰	1.375x10 ⁻¹⁰
concentrations trans- ferred/c. 1000 sec/ cm ²	0.774x10 ⁻⁹	0.67x10 ⁻⁹	0.791x10 ⁻⁹	0.6x10 ⁻⁹
Potential diff. in mv. 1000 sec. after live conc (a. 11-b)	1.44	0.86	1.5	1.66
Potential diff. in mv., capacitance and resistance. (Eq. 11-c)	22.86	31.53	24.45	17.25

TABLE II

Run number	13	14	17	18
Date	2/22/51	3/22/51	3/10/51	3/17/51
Height of petiole in cm.	44.2	17.5	9.2	11.4
Length of venter in cm.	54	20.5	17	14
Height of style-sect. seg.	41.5	20.0	10.4	10.2
Length of style-sect. seg.	21	21.2	25	19
Volume of beetle sol. in ml.	14.9	12.75	17.5	17.5
$(dn/dt)_0$	23.4	11.43	5.05	4.59
$(dn/dt)_0$	20.5	6.42	2.55	2.14
$(dn/dt)_7$	15.15	7.15	4.11	1.02
t_0-t_0 (min)	90	65	110	73
t_0-t_0 (min)	81	54	26	73
t_7-t_0 (min)	43	42	84	56
f_1 -delay factor	1.0712	1.0315	1.0575	1.0514

Product Name	Quantity	Unit Price	Total Price
1. 1000	1000	1.00	1000.00
2. 2000	2000	2.00	4000.00
3. 3000	3000	3.00	9000.00
4. 4000	4000	4.00	16000.00
5. 5000	5000	5.00	25000.00
6. 6000	6000	6.00	36000.00
7. 7000	7000	7.00	49000.00
8. 8000	8000	8.00	64000.00
9. 9000	9000	9.00	81000.00
10. 10000	10000	10.00	100000.00
11. 11000	11000	11.00	121000.00
12. 12000	12000	12.00	144000.00
13. 13000	13000	13.00	169000.00
14. 14000	14000	14.00	196000.00
15. 15000	15000	15.00	225000.00
16. 16000	16000	16.00	256000.00
17. 17000	17000	17.00	289000.00
18. 18000	18000	18.00	324000.00
19. 19000	19000	19.00	361000.00
20. 20000	20000	20.00	400000.00
21. 21000	21000	21.00	441000.00
22. 22000	22000	22.00	484000.00
23. 23000	23000	23.00	529000.00
24. 24000	24000	24.00	576000.00
25. 25000	25000	25.00	625000.00
26. 26000	26000	26.00	676000.00
27. 27000	27000	27.00	729000.00
28. 28000	28000	28.00	784000.00
29. 29000	29000	29.00	841000.00
30. 30000	30000	30.00	900000.00
31. 31000	31000	31.00	961000.00
32. 32000	32000	32.00	1024000.00
33. 33000	33000	33.00	1089000.00
34. 34000	34000	34.00	1156000.00
35. 35000	35000	35.00	1225000.00
36. 36000	36000	36.00	1296000.00
37. 37000	37000	37.00	1369000.00
38. 38000	38000	38.00	1444000.00
39. 39000	39000	39.00	1521000.00
40. 40000	40000	40.00	1600000.00
41. 41000	41000	41.00	1681000.00
42. 42000	42000	42.00	1764000.00
43. 43000	43000	43.00	1849000.00
44. 44000	44000	44.00	1936000.00
45. 45000	45000	45.00	2025000.00
46. 46000	46000	46.00	2116000.00
47. 47000	47000	47.00	2209000.00
48. 48000	48000	48.00	2304000.00
49. 49000	49000	49.00	2401000.00
50. 50000	50000	50.00	2500000.00
51. 51000	51000	51.00	2601000.00
52. 52000	52000	52.00	2704000.00
53. 53000	53000	53.00	2809000.00
54. 54000	54000	54.00	2916000.00
55. 55000	55000	55.00	3025000.00
56. 56000	56000	56.00	3136000.00
57. 57000	57000	57.00	3249000.00
58. 58000	58000	58.00	3364000.00
59. 59000	59000	59.00	3481000.00
60. 60000	60000	60.00	3600000.00
61. 61000	61000	61.00	3721000.00
62. 62000	62000	62.00	3844000.00
63. 63000	63000	63.00	3969000.00
64. 64000	64000	64.00	4096000.00
65. 65000	65000	65.00	4225000.00
66. 66000	66000	66.00	4356000.00
67. 67000	67000	67.00	4489000.00
68. 68000	68000	68.00	4624000.00
69. 69000	69000	69.00	4761000.00
70. 70000	70000	70.00	4900000.00
71. 71000	71000	71.00	5041000.00
72. 72000	72000	72.00	5184000.00
73. 73000	73000	73.00	5329000.00
74. 74000	74000	74.00	5476000.00
75. 75000	75000	75.00	5625000.00
76. 76000	76000	76.00	5776000.00
77. 77000	77000	77.00	5929000.00
78. 78000	78000	78.00	6084000.00
79. 79000	79000	79.00	6241000.00
80. 80000	80000	80.00	6400000.00
81. 81000	81000	81.00	6561000.00
82. 82000	82000	82.00	6724000.00
83. 83000	83000	83.00	6889000.00
84. 84000	84000	84.00	7056000.00
85. 85000	85000	85.00	7225000.00
86. 86000	86000	86.00	7396000.00
87. 87000	87000	87.00	7569000.00
88. 88000	88000	88.00	7744000.00
89. 89000	89000	89.00	7921000.00
90. 90000	90000	90.00	8100000.00
91. 91000	91000	91.00	8281000.00
92. 92000	92000	92.00	8464000.00
93. 93000	93000	93.00	8649000.00
94. 94000	94000	94.00	8836000.00
95. 95000	95000	95.00	9025000.00
96. 96000	96000	96.00	9216000.00
97. 97000	97000	97.00	9409000.00
98. 98000	98000	98.00	9604000.00
99. 99000	99000	99.00	9801000.00
100. 100000	100000	100.00	10000000.00

Total Price

1000000.00

TABLE II--(CONT'D)

Run Number	15	16	17	18
f_2 -decay factor	1.0617	1.0461	1.0704	1.0708
f_3 -decay factor	1.0000	1.0025	1.0068	1.0078
$(dn/dt)_1 f_1$	22.15	19.05	3.47	4.37
$(dn/dt)_2 f_2$	21.3	1.53	2.305	2.30
$(dn/dt)_3 f_3$	1070	740	4.9	1100
He loss in bath vol./ml.	10.1x10 ⁻¹⁰	5.0x10 ⁻¹⁰	7.3x10 ⁻¹⁰	14.2x10 ⁻¹⁰
Ratio of He conc. to $(dn/dt)_3 f_3$	7.9x10 ⁻¹⁰	1.85x10 ⁻¹⁰	1.71x10 ⁻¹⁰	2.12x10 ⁻¹⁰
He loss measured by control (see pg. 10)	2.5x10 ⁻¹⁰	4.0x10 ⁻¹⁰	5.1x10 ⁻¹⁰	2.41x10 ⁻¹⁰
He loss (corrected stirrer, see sect. refer to III)	2.15x10 ⁻¹⁰	10.4x10 ⁻¹⁰	5.1x10 ⁻¹⁰	2.41x10 ⁻¹⁰
He loss absorbed at 15.4x10 ⁻¹⁰ sec. (see sect. refer to III)	10.4x10 ⁻¹⁰	10.7x10 ⁻¹⁰	5.0x10 ⁻¹⁰	2.08x10 ⁻¹⁰
He loss taken up by section	7.4x10 ⁻¹⁰	4.44x10 ⁻¹⁰	2.14x10 ⁻¹⁰	1.32x10 ⁻¹⁰
Total surface area of fibres in cm ²	1.80	21.4	11.9	15.9

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TABLE 11-(CONT'D)

run number	19	20	21	22
Date	1/18/51	1/27/51	2/1/51	2/2/51
weight of control in AS.	17.8	19.6	3.4	19.8
length of control in cm.	22.6	14	9	20
width of white section.	2.9	22.0	3.9	14.0
length of white section.	21	21	13	19.5
vol of bath sol. in ml.	10.5	10.5	13.6	10.5
(c_0/c_0) ₁	10.0	26.6	5.64	5.57
(c_0/c_0) ₂	9.9	17.3	5.85	5.014
(c_0/c_0) ₃	275.2	3012	1250	829
t_0-t_0 (min)	365	32	30	35
t_0-t_0 (min)	378	53	30	32
t_7-t_0 (min)	334	115	130	43
f_1 -decay factor	1.895	1.0247	1.0712	1.0429

Number	Year	Month	Day	Time	Place
1	1870	Jan	1	10:00	St. Louis
2	1870	Jan	2	10:00	St. Louis
3	1870	Jan	3	10:00	St. Louis
4	1870	Jan	4	10:00	St. Louis
5	1870	Jan	5	10:00	St. Louis
6	1870	Jan	6	10:00	St. Louis
7	1870	Jan	7	10:00	St. Louis
8	1870	Jan	8	10:00	St. Louis
9	1870	Jan	9	10:00	St. Louis
10	1870	Jan	10	10:00	St. Louis
11	1870	Jan	11	10:00	St. Louis
12	1870	Jan	12	10:00	St. Louis
13	1870	Jan	13	10:00	St. Louis
14	1870	Jan	14	10:00	St. Louis
15	1870	Jan	15	10:00	St. Louis
16	1870	Jan	16	10:00	St. Louis
17	1870	Jan	17	10:00	St. Louis
18	1870	Jan	18	10:00	St. Louis
19	1870	Jan	19	10:00	St. Louis
20	1870	Jan	20	10:00	St. Louis
21	1870	Jan	21	10:00	St. Louis
22	1870	Jan	22	10:00	St. Louis
23	1870	Jan	23	10:00	St. Louis
24	1870	Jan	24	10:00	St. Louis
25	1870	Jan	25	10:00	St. Louis
26	1870	Jan	26	10:00	St. Louis
27	1870	Jan	27	10:00	St. Louis
28	1870	Jan	28	10:00	St. Louis
29	1870	Jan	29	10:00	St. Louis
30	1870	Jan	30	10:00	St. Louis
31	1870	Jan	31	10:00	St. Louis

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Table 11-(Cont'd)

Run number	14	16	17	20
I_2 -dose, factor	1.5004	1.777	1.0010	1.0005
I_3 -dose, factor	1.1004	1.0018	1.1018	1.0000
$(\sigma_1/\sigma_2)_{I_1}$	65.00	57.50	5.00	5.00
$(\sigma_1/\sigma_2)_{I_2}$	13.10	13.25	1.15	1.00
$(\sigma_1/\sigma_2)_{I_3}$	13.00	5.00	1.70	0.00
ratio of σ_1 to σ_2 with sol./wt.	7.14x10 ¹⁰	6.31x10 ¹⁰	7.14x10 ¹⁰	7.14x10 ¹⁰
ratio of σ_1 to σ_2 by (4-10) ηF_2	6.7x10 ¹⁰	4.11x10 ¹⁰	5.8x10 ¹⁰	5.8x10 ¹⁰
σ_1 ions absorbed by control per sq.	1.00x10 ¹⁶	2.00x10 ¹⁶	2.40x10 ¹⁶	2.10x10 ¹⁶
σ_1 ions present after 30 sec. exp.	11.00x10 ¹⁷	5.7x10 ¹⁷	5.10x10 ¹⁷	5.8x10 ¹⁷
σ_1 ions absorbed after 30 sec. exp. before (No. III)	3.82x10 ¹⁷	4.60x10 ¹⁷	2.10x10 ¹⁷	2.00x10 ¹⁷
σ_1 ions absorbed up to surface	5.00x10 ¹⁷	1.00x10 ¹⁷	0.940x10 ¹⁷	2.32x10 ¹⁷
Total surface area of films in cm ²	10.00	20.0	12.94	10.42

ST	IT	AT	GT	English name
ST1	ST1	ST1	ST1	ST1
ST2	ST2	ST2	ST2	ST2
ST3	ST3	ST3	ST3	ST3
ST4	ST4	ST4	ST4	ST4
ST5	ST5	ST5	ST5	ST5
ST6	ST6	ST6	ST6	ST6
ST7	ST7	ST7	ST7	ST7
ST8	ST8	ST8	ST8	ST8
ST9	ST9	ST9	ST9	ST9
ST10	ST10	ST10	ST10	ST10

Run number	19	20	21	22
See loss based up per section per stimulus	1.0×10^{-12}	6.0×10^{-15}	6.0×10^{-14}	1.0×10^{-13}
See loss based up by section /stimulus/cm	6.0×10^{-10}	1.0×10^{-10}	1.0×10^{-10}	6.0×10^{-10}
Values of the same 20, up sect. /stim/cm	6.0×10^{-11}	1.0×10^{-11}	1.0×10^{-11}	6.0×10^{-11}
See loss based up by section /stim/cm	7.0×10^{-11}	1.0×10^{-11}	1.0×10^{-11}	1.0×10^{-11}
Values of the same 20, up sect. /stim/cm	1.0×10^{-10}	1.0×10^{-10}	1.0×10^{-10}	1.0×10^{-10}
See loss based up by section /stim/cm	1.0×10^{-10}	1.0×10^{-10}	1.0×10^{-10}	1.0×10^{-10}
See loss based up by section /stim/cm	1.0×10^{-10}	1.0×10^{-10}	1.0×10^{-10}	1.0×10^{-10}
Potential diff. in mv. pure capacitive case (20, 20-2)	4.45	4.45	4.45	4.45
Potential diff. in mv. capacitive and resistive case (20, 20-2)	10.15	10.15	10.15	10.15

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TABLE II-(CONT'D)

Run Number	25	24	23	22
Date	1-22-51	1-20-51	1-20-51	1-21-51
Weight of control to mg.	38.0	41.0	37.0	36.5
Length of reaction to sec.	27	34	28	27.5
Weight of stim. shot, mg.	71.2	74.4	72.2	71.4
Length of stim. reaction	24		29	29.5
Vol. of bath sol. in cu.	34.1	34.0	34.3	34.5
$(dm/dt)_d$	11.53	27.0	22.5	34.0
$(dm/dt)_g$	3.67	16.2	15.48	27.0
$(\bar{c}/\Delta t)_g$	229.5	1199	939	1179
$t_g - t_0$ (abs)	53	32	152	41
$t_d - t_0$ (abs)	27	27	115	37
$t_g - t_d$ (abs)	27	9	39	21
f_1 -factor factor	1.6416	1.625	1.6373	1.632

TABLE II-(CONT'D)

Run Number	23	24	25	26
f_2 -decay factor	1.0230	1.000	1.0016	1.0036
f_3 -decay factor	1.0206	1.008	1.005	1.015
$(dn/dt)_{f_1}$	12.13	59.4	84.7	88.7
$(dn/dt)_{f_2}$	9.72	55.6	81.2	83.7
$(dn/dt)_{f_3}$	331.9	1500	915	1152
Na ions in bath sol/ml.	7.14x10 ¹⁹	6.9 x10 ¹⁹	7.015x10 ¹⁹	6.493x10 ¹⁹
Ratio of Na conc. to $(dn/dt)_{f_3}$	18.0x10 ¹⁶	5.41x10 ¹⁶	7.9x10 ¹⁶	3.64x10 ¹⁶
Na ions adsorbed by control per mg.	2.51x10 ¹⁶	-----	-----	10.68x10 ¹⁶
Na ions present stim. nerve sect.	21.85x10 ¹⁷	-----	-----	37.59x10 ¹⁷
Na ions adsorbed stim. nerve sect. Refer (Eq. III)	20.85x10 ¹⁷	-----	-----	31.25x10 ¹⁷
Na ions taken up by section	1.0x10 ¹⁷	-----	-----	4.34x10 ¹⁷
Total surface area of fibres in cm ²	0.85	-----	-----	14.4

TABLE II-(CONT'D)

Run number	23	24	25	26
As ions taken up per section per stimulus	12 0.143x10	-----	-----	12 1.44x10
As ions taken up per section / stimulus/cm ²	10 1.013x10	-----	-----	10 6.92x10
moles of As taken up by sect. / stimulus/cm ²	-13 0.153x10	-----	-----	-13 0.984x10
As ions taken up by sect/sec/cm ²	13 2.2x10	-----	-----	13 12.94x10
moles of As taken up by sect / sec/cm ²	-10 0.369x10	-----	-----	-10 2.16x10
Coulombs transferred/sec/cm ²	-9 6.1623x10	-----	-----	-3 0.244x10
Potential diff. in mv., pure capacit-ive case (Eq. II-5)	1.36	-----	-----	7.90
Potential diff. in mv., capacitance and resistance (Eq. II-3)	5.0	-----	-----	29.2

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TABLE III

SPLICE ACCEPTANCE DATA FOR THREE FANTIONS - SERIAL F1-13.

Run No.	Time min.	Weight of spec. sect. in mg.	Length in mm.	Activity in cps per mg.	Number of iodine ions adsorbed per mg. of titanium wet. ¹⁶
1	5	7.5	7.0	0.441	4.18×10^{16}
2	10	7.0	7.0	0.585	5.75×10^{16}
3	15	9.5	7.0	0.591	5.72×10^{16}
4	20	7.1	6.5	0.682	6.6×10^{16}
5	30	4.4	4.5	0.242	2.30×10^{16}
6	40	4.4	7.5	0.704	6.24×10^{16}
7	50	5.3	10.0	0.320	3.07×10^{16}
8	60	3.6	5.0	0.980	9.65×10^{16}
9	75	3.6	3.0	0.800	7.36×10^{16}
10	90	3.4	7.0	1.025	10.1×10^{16}
11	95	7.0	7.0	1.050	10.55×10^{16}
12	110	7.0	7.0	1.00	9.86×10^{16}
13	130	3.6	4.5	1.060	10.46×10^{16}

TABLE IV
SURFACE ABSORPTION DATA FOR NERVE SECTIONS - NARA CRYSTALLINE

Run No.	Time in min.	Weight of nerve sect. in mg. (wet)	Length in mm.	Activity in cps p r sq.	Number of Sodium Ions adsorbed per sq. of tissue wet
1	10	2.2	4	0.445	5.5×10^{16}
2	20	2.2	3.5	0.522	2.5×10^{16}
3	30	4.2	7.0	0.554	2.5×10^{16}
4	43	7.6	7.5	0.490	3.5×10^{16}
5	60	8.5	8.5	0.575	4.1×10^{16}
6	80	11.5	12	0.635	3.9×10^{16}
7	70	4.8	5.5	0.522	2.5×10^{16}
8	77	5.0	11.5	0.965	3.0×10^{16}
9	90	10.3	9.5	0.345	2.1×10^{16}
10	100	10.0	9.5	0.628	3.7×10^{16}

Each solution contained 7.134×10^{19} atoms of sodium per ml., with a ratio of concentration to activity of 5.61×10^{16} atoms sodium per cps.

TABLE VI

Summary of results of the study of the effect of the concentration of the reagent on the rate of the reaction

Concentration of reagent, mole/l.	Rate of reaction, mole/l. sec.	Order of reaction	Order of reaction with respect to reagent
0.001	0.001	1	1
0.002	0.002	1	1
0.003	0.003	1	1
0.004	0.004	1	1
0.005	0.005	1	1
0.006	0.006	1	1
0.007	0.007	1	1
0.008	0.008	1	1
0.009	0.009	1	1
0.010	0.010	1	1
0.011	0.011	1	1
0.012	0.012	1	1
0.013	0.013	1	1
0.014	0.014	1	1
0.015	0.015	1	1
0.016	0.016	1	1
0.017	0.017	1	1
0.018	0.018	1	1
0.019	0.019	1	1
0.020	0.020	1	1
0.021	0.021	1	1
0.022	0.022	1	1
0.023	0.023	1	1
0.024	0.024	1	1
0.025	0.025	1	1
0.026	0.026	1	1
0.027	0.027	1	1
0.028	0.028	1	1
0.029	0.029	1	1
0.030	0.030	1	1
0.031	0.031	1	1
0.032	0.032	1	1
0.033	0.033	1	1
0.034	0.034	1	1
0.035	0.035	1	1
0.036	0.036	1	1
0.037	0.037	1	1
0.038	0.038	1	1
0.039	0.039	1	1
0.040	0.040	1	1
0.041	0.041	1	1
0.042	0.042	1	1
0.043	0.043	1	1
0.044	0.044	1	1
0.045	0.045	1	1
0.046	0.046	1	1
0.047	0.047	1	1
0.048	0.048	1	1
0.049	0.049	1	1
0.050	0.050	1	1
0.051	0.051	1	1
0.052	0.052	1	1
0.053	0.053	1	1
0.054	0.054	1	1
0.055	0.055	1	1
0.056	0.056	1	1
0.057	0.057	1	1
0.058	0.058	1	1
0.059	0.059	1	1
0.060	0.060	1	1
0.061	0.061	1	1
0.062	0.062	1	1
0.063	0.063	1	1
0.064	0.064	1	1
0.065	0.065	1	1
0.066	0.066	1	1
0.067	0.067	1	1
0.068	0.068	1	1
0.069	0.069	1	1
0.070	0.070	1	1
0.071	0.071	1	1
0.072	0.072	1	1
0.073	0.073	1	1
0.074	0.074	1	1
0.075	0.075	1	1
0.076	0.076	1	1
0.077	0.077	1	1
0.078	0.078	1	1
0.079	0.079	1	1
0.080	0.080	1	1
0.081	0.081	1	1
0.082	0.082	1	1
0.083	0.083	1	1
0.084	0.084	1	1
0.085	0.085	1	1
0.086	0.086	1	1
0.087	0.087	1	1
0.088	0.088	1	1
0.089	0.089	1	1
0.090	0.090	1	1
0.091	0.091	1	1
0.092	0.092	1	1
0.093	0.093	1	1
0.094	0.094	1	1
0.095	0.095	1	1
0.096	0.096	1	1
0.097	0.097	1	1
0.098	0.098	1	1
0.099	0.099	1	1
0.100	0.100	1	1

The rate of reaction was measured by the method of initial rates. The concentration of the reagent was varied from 0.001 to 0.100 mole/l. The rate of reaction was found to be independent of the concentration of the reagent. The order of reaction with respect to the reagent was found to be 1. The rate of reaction was found to be independent of the concentration of the reagent. The order of reaction with respect to the reagent was found to be 1.

TABLE V

SUMMARY OF OBSERVED DATA

Run No.	Period of stimulation	Area under curve by sect, /stimulus/cm ²	Area taken up by sect, sect./stim./cm ²	Area of Ia taken up by sect./stim./cm ²	Coulombs trans- ferred/stimulus/ cm ²	Voltage diff. (a) (b)
1	15'40"	8.74x10 ⁻¹⁰	1.25x10 ⁻¹¹	1.25x10 ⁻¹¹	1.53x10 ⁻⁸	12.25 40.2
2	"	7.59x10 ⁻¹⁰	1.27x10 ⁻¹³	1.27x10 ⁻¹¹	1.23x10 ⁻⁸	10.25 38.0
3	"	10.27x10 ⁻¹⁰	1.75x10 ⁻¹¹	1.75x10 ⁻¹⁰	1.64x10 ⁻⁸	12.55 39.2
4	"	10.20x10 ⁻¹⁰	1.75x10 ⁻¹¹	1.75x10 ⁻¹⁰	1.69x10 ⁻⁸	14.06 52.2
5	"	9.47x10 ⁻¹⁰	1.65x10 ⁻¹³	1.65x10 ⁻¹⁰	1.50x10 ⁻⁸	12.55 40.3
Average values		8.57x10 ⁻¹⁰	1.59x10 ⁻¹³	1.59x10 ⁻¹⁰	1.53x10 ⁻⁸	12.72 47.2
6	20'20"	15.5x10 ⁻¹⁰	2.55x10 ⁻¹³	2.55x10 ⁻¹⁰	2.45x10 ⁻⁸	20.55 78.1
7	"	12.2x10 ⁻¹⁰	1.77x10 ⁻¹³	1.77x10 ⁻¹⁰	1.51x10 ⁻⁸	11.0 40.3
8	"	10.24x10 ⁻¹⁰	1.95x10 ⁻¹³	1.95x10 ⁻¹⁰	1.75x10 ⁻⁸	14.6 52.5
9	"	9.2x10 ⁻¹⁰	1.54x10 ⁻¹³	1.54x10 ⁻¹⁰	1.48x10 ⁻⁸	12.4 45.2
10	"	15.4x10 ⁻¹⁰	2.56x10 ⁻¹³	2.56x10 ⁻¹⁰	2.45x10 ⁻⁸	20.55 78.1
Average values		11.25x10 ⁻¹⁰	1.97x10 ⁻¹³	1.97x10 ⁻¹⁰	1.89x10 ⁻⁸	15.82 58.6

TABLE V (continued)

run no.	period of stimulation of Fe^{2+} solution/cell	moles of Fe taken up by Fe^{2+} sol./cell/cm ²	coultombs consumed/cell/cm ²	voltage diff. mv.
11	60' 1.88×10^{-10}	0.90×10^{-13}	0.774×10^{-3}	3.44
12	" 1.57×10^{-10}	0.78×10^{-13}	0.89×10^{-3}	4.52
13	" 1.34×10^{-10}	0.88×10^{-13}	0.79×10^{-3}	3.65
14	" 0.8×10^{-10}	0.68×10^{-13}	0.66×10^{-3}	4.56
Average Value	1.41×10^{-10}	0.76×10^{-13}		<u>3.88</u>
				<u>104</u>

NUMBER	DATE	DESCRIPTION	AMOUNT	BALANCE
14	7	to cash	100.00	100.00
15	8	to cash	100.00	200.00
16	9	to cash	100.00	300.00
17	10	to cash	100.00	400.00
18	11	to cash	100.00	500.00

and not included in the balance sheet as of 12/31/1917

TABLE VI

LIST OF EXPERIMENTAL EQUIPMENT

The following apparatus was made available by Dr. Eric Ogden of the Department of Physiology, The Ohio State University or purchased on U.S. Navy contract.

(1) Stimulation Unit Model 3 B	Grass Instrument Co.
(2) Stimulation Isolation Unit	Grass Instrument Co.
(3) Geiger Mueller Tube Model TAC-1 Serial 14725 R.T. 2.1 $\mu\text{g}/\text{cm}^2$	Tracer Lab., Inc.
(4) Pre-amplifier Unit Mod. P4	Grass Instrument Co.
(5) Cathode-ray Oscilloscope. Mod. 404	A.B. Dufont Lab. Inc.
(6) Radio Assay Sample Holder Mod. 40-10a	Tracer Lab. Inc.
(7) Auto Reader 40-15	Tracer Lab. Inc.
(8) Platinum Electrode Nerve Stimulation Platinum	Medical Shop Hamilton Mall, U.S.U.
(9) Glass Nerve Chambers	Glass Blowing Shop, Dept. of Chemistry, U.S.U.

LIST OF

THE UNIVERSITY OF CHICAGO

The following is a list of the names of the persons who have been members of the University of Chicago since its organization in 1890. The names are arranged in alphabetical order of the last name.

(1) ALABAMA STATE UNIVERSITY

ALABAMA

(2) ALABAMA STATE UNIVERSITY

ALABAMA

(3) ALABAMA STATE UNIVERSITY

ALABAMA

ALABAMA

ALABAMA

(4) ALABAMA STATE UNIVERSITY

ALABAMA

(5) ALABAMA STATE UNIVERSITY

ALABAMA

(6) ALABAMA STATE UNIVERSITY

ALABAMA

ALABAMA

ALABAMA

(7) ALABAMA STATE UNIVERSITY

ALABAMA

(8) ALABAMA STATE UNIVERSITY

ALABAMA

(9) ALABAMA STATE UNIVERSITY

(10) ALABAMA STATE UNIVERSITY

- | | | |
|------|--|---|
| (10) | Lead Shielding
Grices (23)
4" x 8" x 5" | Tracer Lab., Inc.
Medical Shop, Hamilton
Hall, O.S.U. |
| (11) | Remote Pipetting Device
Mod. K-16 | Tracer Lab., Inc. |
| (12) | Remote Handling Tongs
Mod. K-17 | Tracer Lab., Inc. |
| (13) | Set of Al. absorbers
Mod. K-18 | Tracer Lab., Inc. |
| (14) | Radioactive Reference
Source Co ⁶⁰ Cat. No. R-19 | Tracer Lab., Inc. |
| (15) | Cupped Assay Planchets
Mod. E-20 | Tracer Lab., Inc. |
| (16) | Five Ring Stands | Dept. of Physiology, O.S.U. |
| (17) | Assorted Pyrex Glassware,
graduated, etc. | Dept. of Physiology, O.S.U. |
| (18) | Taigon Tubing
10 feet, I.D. = 3 mm. | Dept. of Physiology, O.S.U. |
| (19) | Film Type Dosimetry Badge | Dr. W. Rogers
Health physicist, O.S.U. |

(10)	1900-1901	1900-1901
(11)	1901-1902	1901-1902
(12)	1902-1903	1902-1903
(13)	1903-1904	1903-1904
(14)	1904-1905	1904-1905
(15)	1905-1906	1905-1906
(16)	1906-1907	1906-1907
(17)	1907-1908	1907-1908
(18)	1908-1909	1908-1909
(19)	1909-1910	1909-1910
(20)	1910-1911	1910-1911
(21)	1911-1912	1911-1912
(22)	1912-1913	1912-1913
(23)	1913-1914	1913-1914
(24)	1914-1915	1914-1915
(25)	1915-1916	1915-1916
(26)	1916-1917	1916-1917
(27)	1917-1918	1917-1918
(28)	1918-1919	1918-1919
(29)	1919-1920	1919-1920
(30)	1920-1921	1920-1921
(31)	1921-1922	1921-1922
(32)	1922-1923	1922-1923
(33)	1923-1924	1923-1924
(34)	1924-1925	1924-1925
(35)	1925-1926	1925-1926
(36)	1926-1927	1926-1927
(37)	1927-1928	1927-1928
(38)	1928-1929	1928-1929
(39)	1929-1930	1929-1930
(40)	1930-1931	1930-1931
(41)	1931-1932	1931-1932
(42)	1932-1933	1932-1933
(43)	1933-1934	1933-1934
(44)	1934-1935	1934-1935
(45)	1935-1936	1935-1936
(46)	1936-1937	1936-1937
(47)	1937-1938	1937-1938
(48)	1938-1939	1938-1939
(49)	1939-1940	1939-1940
(50)	1940-1941	1940-1941
(51)	1941-1942	1941-1942
(52)	1942-1943	1942-1943
(53)	1943-1944	1943-1944
(54)	1944-1945	1944-1945
(55)	1945-1946	1945-1946
(56)	1946-1947	1946-1947
(57)	1947-1948	1947-1948
(58)	1948-1949	1948-1949
(59)	1949-1950	1949-1950
(60)	1950-1951	1950-1951
(61)	1951-1952	1951-1952
(62)	1952-1953	1952-1953
(63)	1953-1954	1953-1954
(64)	1954-1955	1954-1955
(65)	1955-1956	1955-1956
(66)	1956-1957	1956-1957
(67)	1957-1958	1957-1958
(68)	1958-1959	1958-1959
(69)	1959-1960	1959-1960
(70)	1960-1961	1960-1961
(71)	1961-1962	1961-1962
(72)	1962-1963	1962-1963
(73)	1963-1964	1963-1964
(74)	1964-1965	1964-1965
(75)	1965-1966	1965-1966
(76)	1966-1967	1966-1967
(77)	1967-1968	1967-1968
(78)	1968-1969	1968-1969
(79)	1969-1970	1969-1970
(80)	1970-1971	1970-1971
(81)	1971-1972	1971-1972
(82)	1972-1973	1972-1973
(83)	1973-1974	1973-1974
(84)	1974-1975	1974-1975
(85)	1975-1976	1975-1976
(86)	1976-1977	1976-1977
(87)	1977-1978	1977-1978
(88)	1978-1979	1978-1979
(89)	1979-1980	1979-1980
(90)	1980-1981	1980-1981
(91)	1981-1982	1981-1982
(92)	1982-1983	1982-1983
(93)	1983-1984	1983-1984
(94)	1984-1985	1984-1985
(95)	1985-1986	1985-1986
(96)	1986-1987	1986-1987
(97)	1987-1988	1987-1988
(98)	1988-1989	1988-1989
(99)	1989-1990	1989-1990
(100)	1990-1991	1990-1991

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Bennett

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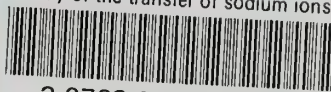
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